INTRA-COLONY VARIATION IN BREEDING SUCCESS OF ATLANTIC PUFFINS: AN APPLICATION OF HABITAT SELECTION THEORY

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ABSTRACT

Theoretical models of habitat selection generally assume that organisms behave optimally, that population density correlates with resource abundance, and that increasing density reduces habitat quality. My purpose was to determine whether current models could explain the distribution of Atlantic Puffins (*Fratercula arctica*) breeding on Great Island, Newfoundland and, if not, to propose a model that could. Theoretical models have rarely been applied to explain the distribution of a colonially-nesting species that may gain fitness benefits from increasing density.

I used breeding success as a representative measure of fitness that I compared among three habitats, maritime slope, maritime level, and inland slope, sampled at three locations, north, east and south on Great Island in 1992 and 1993. Based on results of previous studies, I predicted that distance from the shore edge of the colony, slope, and aspect would be the most important habitat variables that discriminate habitat quality for puffins on Great Island.

Nest density was highest in maritime slope and lowest in inland slope habitat and was best predicted by distance from the shore edge of the colony. Breeding success, as measured by the proportions of burrows that fledged chicks, was highest in maritime and inland slope habitats and lowest in maritime level habitat and was related to distance from the edge and slope. Aspect was an important predictor of timing of breeding but was not significantly related to breeding success. Thus, it

appeared that preferred areas were close to shore, while optimal areas were on slopes.

High breeding success and nest density in maritime slope habitat was predicted by current habitat selection models, but high success at low density in inland slope habitat was not. Breeding success increased with density within habitats, also contrary to model predictions. Current models proved unable to explain the distribution of puffins if breeding success was used as the sole measure of fitness. A cost-benefit model is proposed that acknowledges habitat related fitness costs that are not accounted for by typical measures of breeding success. Unique cost-benefit ratios for different habitats can explain observed patterns of dispersion and breeding success.

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INTRODUCTION

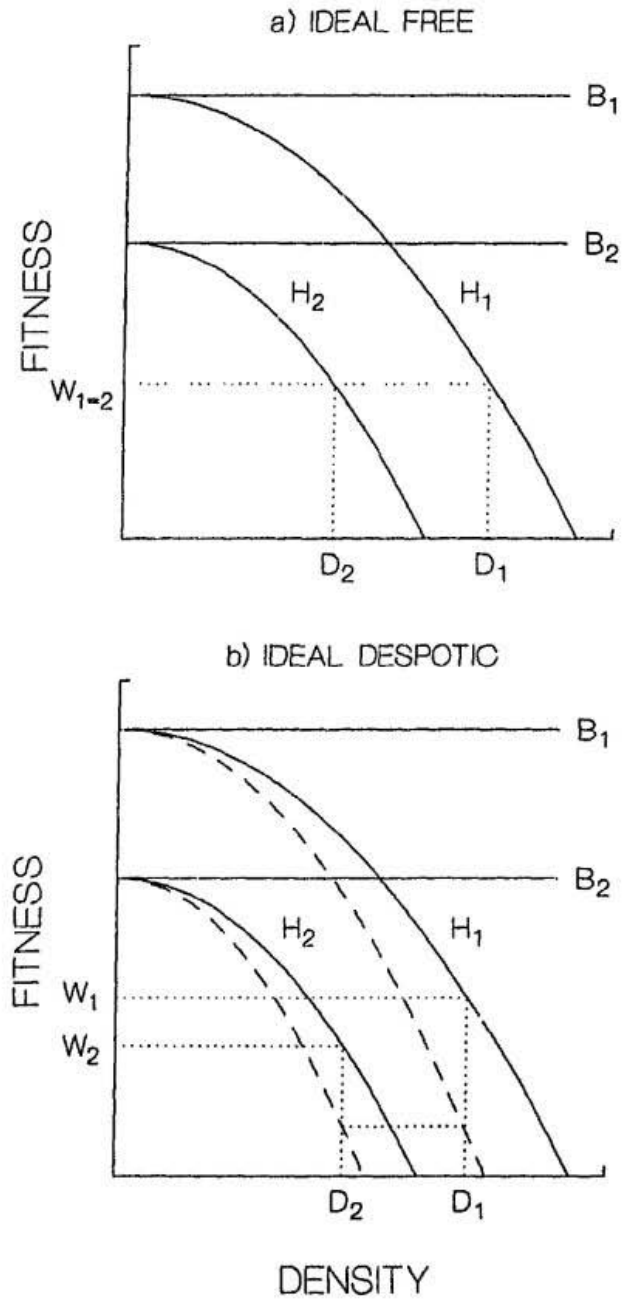
1.1. Habitat selection theory

Habitat selection theory attempts to predict the spatial and temporal distribution of organisms (e.g., Fretwell 1972) using the economics of individual fitness (Fisher 1930). Theories explicitly or implicitly assume that individuals will select places to live that maximize fitness (Fretwell and Lucas 1970, Rosenzweig 1981, 1985, 1991, Holt 1987, Morris 1989, 1991). Two initial, density-dependent models, ideal-free and ideal-despotic distributions, proposed by Fretwell and Lucas (1970), incorporated principles of optimal foraging and intraspecific competition (Svardson 1949, Kluyver and Tinbergen 1953, Emlen 1966, MacArthur and Pianka 1966, Brown 1969). "Ideal" individuals have perfect knowledge of their environment (e.g., food supply in different habitats) and incur no costs in sampling or moving among habitats. Models assume that habitat quality declines with increasing consumer density due to factors such as increased predator activity and competition for food (Fretwell and Lucas 1970). In an ideal-free distribution, individuals can freely choose and move among habitats, and should distribute themselves such that mean fitness is the same across habitats (Fig. 1a; see also Parker 1970, 1974). Alternately, fitness will not be equal across habitats if established individuals are "despotic" and can maintain higher fitness in a preferred habitat by excluding others (ideal-despotic distribution; Fig. 1b). Higher fitness in a preferred habitat does not

result from differences in competitive ability between established and recruiting individuals (see Łomnicki 1988), but only to the collective effect of territorial behaviour by established individuals. All individuals are assumed to have equal competitive abilities in both ideal-free and ideal-despotic models.

Although some of the assumptions of these initial models were unrealistic (Fretwell and Lucas 1970), ideal-free and ideal-despotic models provided useful predictions for habitat selection studies (e.g., Pierotti 1982, Morris 1989, Halama and Dueser 1994) and a framework for further theoretical development. Subsequent elaborations of these models have considered limited knowledge and perceptual ability of "non-ideal" individuals (Stephens and Krebs 1986, Beletsky and Orians 1987, Orians 1991, Englund 1993), sampling and movement costs (Rosenzweig 1974, Charnov 1976, Morris 1987a, Pulliam and Danielson 1991, Englund 1993), variation in degree of density-dependent depression of habitat quality (Morris 1987b, 1988), interspecific competition (Lawlor and Maynard Smith 1976, Rosenzweig 1986, 1991, Morris 1988), predation (Charnov et al. 1976, Sih 1987), interference (Sutherland 1983), and effects of spatial and temporal scale (Istock and Weisburg 1987, Morris 1987a,c, 1991, Orians and Wittenberger 1991, Halama and Dueser 1994). Theories typically assume that population density correlates with resource abundance and highest densities will occur in preferred habitats (Rosenzweig 1991). Consideration of habitat specific demographic rates revealed that resource abundance and consumer density may be decoupled, creating situations where densities can be

FIGURE 1. Comparison between ideal-free and ideal-despotic distributions (after Fretwell and Lucas 1970). Lines B1 and B2 indicate basic fitness values for two habitats of different quality, H1 and H2. First settlers to H1 and H2 will reap fitness benefits B1 and B2, respectively. Fitness-density curves plot realized fitness as a function of density. Differences between realized fitness and basic fitness in each habitat increase as density increases, depicting declining fitness for individuals using a habitat as population density increases. Assuming that individuals will choose the habitat where fitness rewards are greatest, and that they have perfect knowledge of the rewards to be obtained, we can predict how individuals will distribute themselves at different population levels. First settlers to an area will choose only H1 because initial fitness (B1) is higher there than in H2 (B2). In an ideal-free model (a), where there is no resistance to settling individuals (i.e., no territoriality), individuals will continue to settle in H1 until density becomes high enough to reduce realized fitness in H1 to B2, at which point potential fitness in H2 equals that in H1, and individuals will begin to settle in H2. As density increases further, individuals will distribute themselves so as to maintain equal fitness benefits in the two habitats (e.g., W1 = W2 in the two habitats at densities D1 and D2). Note that fitness is equal across habitats and density is greater in the higher quality habitat. In an ideal-despotic model (b), new settlers face territorial resistance from established individuals. Penetrating this resistance entails a fitness cost to settling individuals, and results in a perceived fitness (dashed lines) that is less than the realized fitness obtained after an individual succeeds in settling in a habitat. Because we assume that this cost is related only to the territorial behaviour of established individuals, it is the same in both habitats and increases as the density of established individuals increases. The pattern of settlement as population increases is similar to that predicted under an ideal-free model except that individuals choose the habitat where the perceived rather than the actual fitness is greatest (this poses some conceptual problems with the model - see Discussion). For example, at a given population, individuals will distribute themselves in the two habitats at densities D1 and D2 such that the perceived fitness in the two habitats is the same. However, realized fitness will be higher in H1 than in H2 (W1 > W2). Note that in going from an ideal-free to an ideal-despotic distribution, at a given population size, density in H1 has decreased and density in H2 has increased. In effect, territorial behaviour has prevented some individuals from settling in H1 and forced them into H2.


a) IDEAL FREE
B1
B2
H2
H1
FITNESS
W1=2
D2
D1
b) IDEAL DESPOTIC
B1
B2
H2
H1
FITNESS
W1
W2
D2
D1
DENSITY

higher in "sink" (low-quality) habitats, maintained by immigration from "source" (high-quality) habitats (Lidicker 1975, van Horne 1983, Holt 1987, Pulliam 1988).

Habitat selection is often modelled in relation to foraging behaviour and food availability, but predictions of habitat selection models can be generalized and applied to the distribution of animals with respect to any varying and limited resource. Applied to breeding habitat, most habitat selection models predict that all individuals within a particular habitat will experience equal success. If an ideal-free distribution is operating, individual breeding success will be similar across habitats and nesting density will reflect differences in habitat quality. Under an ideal-despotic distribution, breeding success will vary among habitats and density will reflect differences among habitats as well as dominance behaviour by individuals (see Fig. 1).

The prediction that all individuals within a habitat will experience equal fitness is unlikely to be realized (Fretwell 1972, Davies 1982, Parker 1982, Begon 1984, Pulliam 1989). Individual variation is a constant feature of studies of reproductive performance (e.g., Clutton-Brock 1988, Newton 1989) and studies quoted in support of free distribution models show consistent individual differences within habitats (Parker and Sutherland 1986).

Attempts have been made to incorporate individual differences into habitat selection models. Pulliam and Danielson (1991) modified the ideal free distribution to include persistent differences in the quality of individual breeding sites (ideal

preemptive distribution). In this model, individuals settle in the habitat with the best unoccupied site and occupation of lower quality sites does not depress the quality of better sites, thus maintaining individual differences in reproductive success within habitats. Parker and Sutherland (Parker 1982, Sutherland and Parker 1985, Parker and Sutherland 1986) incorporated individual differences in competitive ability into their phenotype-limited ideal free models (see also Łomnicki 1988, 1992). Within a habitat, individuals gain different fitness benefits according to their competitive abilities. Habitat selection by a particular individual is affected by habitat quality and consumer density as in other models, and also by that individual's ability relative to the abilities of other competitors. Thus, unlike other models which, given the same circumstances, predict the same habitat choices for all individuals, phenotype-limited ideal free models may predict different choices for individuals with different competitive abilities.

Parker and Sutherland (1986) have shown that consideration of individual differences in competitive ability can alter the predictions of ideal-free models. Contrary to predictions of the ideal free model of Fretwell and Lucas, phenotype-limited ideal free models predict that, if individuals interfere with each other, the most competitive individuals will obtain the best sites and average benefits will be higher in the best sites. The relationship between density and habitat quality is more difficult to predict because it depends on the range of competitive abilities in the population, on how density affects interference, and on the way interference affects

benefits of different competitors. Thus, although they may approximate real conditions more closely than simpler models of Fretwell and Lucas, the complexity of interacting factors and the variety of possible predictions of phenotype-limited ideal free models makes them more difficult to test (Parker and Sutherland 1986).

The above models incorporate static measures of individual ability and fitness. Partridge (1978) suggested that habitat related fitness may be dynamic, increasing as an individual gains experience in a particular habitat. This may explain plasticity in habitat choice exhibited by young birds and increased site tenacity shown by experienced and successful breeders (Partridge 1978). She also raised the important problem that if there is competition for preferred habitats, and if animals that can obtain and defend sites in preferred habitat have higher fitness than those excluded, then comparisons between habitats will be confounded by original differences in fitness of individuals that occupy those habitats (e.g. Coulson 1968).

A major assumption of habitat selection models, that average fitness in a habitat declines with increasing consumer density, has not been challenged. Although many researchers have examined potential benefits of colonial breeding, communal roosting, and foraging in flocks (see review in Wittenberger and Hunt 1985), theoretical models have not been applied to explain habitat selection in situations where fitness benefits may increase with density. Fretwell and Lucas (1970, Fretwell 1972) concluded that a positive relationship between fitness and density probably occurs only at low densities (following Allee et al. 1949) and need

not be considered in most circumstances. This is an important assumption to consider in the investigation of a colonial-breeding seabird.

1.2. Seabird breeding biology

Seabirds are particularly interesting animals for investigations of habitat selection theory. The majority of seabird species (98%) nest in colonies, a much higher proportion than any other type of bird (Lack 1968). Breeding and foraging habitats are distinct, meaning that separate habitat choices must be made for those activities. The separation of feeding and breeding habitats simplifies the analysis for selection of breeding habitat, although fitness components related to foraging contribute to breeding success and may complicate the interpretation of nesting habitat differences. Relationships between fitness and nesting density within habitats depend on a variety of costs and benefits associated with colonial breeding. The balance of costs and benefits will determine whether fitness declines with increasing density as assumed by habitat selection models.

1.2.1. Benefits of colonial nesting

1.2.1.1. Availability of food and nest sites

Nesting in colonies may be advantageous if nest sites within commuting distance of food supplies are limited (Lack 1968, Snapp 1976, Birkhead and Furness 1985). Many species, including those of the Alcidae family to which puffins belong,

are awkward on land, making them highly vulnerable to predation. Such species are limited in their choice of nest sites to isolated islands or cliffs that are inaccessible to terrestrial predators (Lack 1968, Montevecchi 1977, Jehl and Mahoney 1987). Some species place their nests in secure locations in burrows or crevices, and are nocturnal on their colonies to further reduce risks from avian predators. Obtaining a safe nest site may provide a net benefit when balanced against the obvious costs of sharing limited habitat (Alexander 1974, Wittenberger and Hunt 1985). Other factors are needed to explain why nesting birds aggregate more than is necessary within available habitat (Hoogland and Sherman 1976, Gochfeld 1980).

1.2.1.2. Predator defence

Colonial nesting enhances predator defence through vigilance, mobbing and swamping tactics (Kruuk 1964, Horn 1968, Lack 1968, Wittenberger and Hunt 1985) and dense aggregations provide cover through "selfish herd" effects (Hamilton 1971). These tactics are more effective in larger groups and when birds are synchronous in their breeding activities (see below). Higher numbers of young produced per pair in large colonies than in small colonies have been reported for a number of species (Tenaza 1971). This may result indirectly from social facilitation leading to greater breeding synchrony and thus more effective predator defense at large colonies (Darling 1938), it may be attributable to differential effects of predation and disturbance at small colonies which have a greater proportion of peripheral nesters

than large colonies (Tenaza 1971), it may be due to a higher proportion of inexperienced breeders at small colonies (Lack 1954), and it may be a result of other factors such as food availability, habitat quality, and interspecific competition (see Hatch and Hatch 1990).

1.2.1.3. Information centre

Birds may benefit from nesting in colonies if they gain information on the location of food that they would not otherwise obtain (Horn 1968, Ward and Zahavi 1973, Emlen and Demong 1975). Evidence that a seabird colony may operate as an information centre was provided by a study of two Common Tern (*Sterna hirundo*) colonies in upstate New York (Waltz 1987). In this study unsuccessful foragers were more likely to follow others than successful foragers, birds that had returned with fish were more likely to be followed than those that did not, birds departed the colony synchronously and towards similar feeding areas, and birds that arrived at feeding areas in groups were more successful at finding food than solitary birds. In other studies there is little direct evidence to support the hypothesis (Gaston and Nettleship 1981, Wittenberger and Hunt 1985).

1.2.1.4. Social facilitation

Social stimulation may enhance territorial behaviour and pair co-ordination (Nelson 1978) and is required by some species in order to breed successfully

(Coulson and Dixon 1979). As mentioned above, social stimulation may increase breeding synchrony, which may be advantageous as an aid to predator defence, but also may be a disadvantage if it increases competition for temporally limited resources (Wittenberger and Hunt 1985). Social facilitation can function only where birds can communicate with each other, and in large colonies will be limited to smaller, interacting subgroups (Coulson and Dixon 1979, Burger and Shisler 1980, Gochfeld 1980, Wanless and Harris 1988).

1.2.1.5. Other benefits

Other potential advantages to colonial nesting include increased access to mates, and greater opportunity for extra-pair copulations, kleptoparasitism, and cannibalism (Hoogland and Sherman 1976, Wittenberger and Hunt 1985).

1.2.2. Costs of colonial nesting

1.2.2.1. Competition for food

Ashmole (1963) suggested that competition for food and depletion of prey could reduce reproductive output at large colonies. Such an effect has been implicated in a number of studies but has yet to be demonstrated. Birkhead and Furness (1985) found that colony size was negatively correlated with the numbers of conspecifics breeding at other colonies within a species foraging range, and also

found a significant relationship between colony size and available foraging area. These relationships can be explained by the distribution of colony sites and do not necessarily imply competition for food (Cairns 1989). Fledging weights have been negatively correlated with colony size of Atlantic Puffins (*Fratercula arctica*) (Gaston 1985) and Thick-billed Murres (*Uria lomvia*) (Gaston et al. 1983, Furness and Barrett 1985), and growth rates, fledging weights, and breeding success have been negatively correlated with population size in other species (Hunt et al. 1986). Hunt et al. (1986) distinguished between population size (numbers of a particular species at a colony), colony size (numbers of all species at a colony), and effective colony size (numbers of those species whose diets were expected to overlap), and found no relationship between reproductive performance and colony size or effective colony size. They concluded that food depletion was not occurring and that the effect of population size could best be explained by an interference mechanism operating when species foraged together in dense aggregations. Prey depletion was indicated by the results of a study by Birt et al. (1987) who found lower densities of prey fish in bays where Double-crested Cormorants (*Phalacrocorax auritus*) were feeding than in adjacent bays. Competition for food is most likely to affect species that feed inshore or nearshore in large concentrations. Competition could vary within a colony in a density-dependant manner if individuals that nest together, feed together.

1.2.2.2. Competition for nest sites

Interspecific competition limits nesting distributions and, ultimately, has contributed to the evolution of habitat partitioning among species (Belopol'skii 1957, Hilden 1965, Klopfer and Hailman 1965, Lack 1968, Bedard 1969, Trivelpiece and Volkman 1979, Knudtson and Byrd 1982, Squibb and Hunt 1983, Birkhead and Nettleship 1987, Olsthoorn and Nelson 1990, Wallace et al. 1992). If nest sites are limited, competitive exclusion will narrow the range of choices available to species less able to compete. Competition between Manx Shearwaters (*Puffinus puffinus*) and puffins on Skomer Island resulted in the exclusion of some puffins from burrows and lowered breeding success of both species in areas where they shared burrows (Ashcroft 1979, Harris 1984). Expanding Common Murre (*Uria aalge*) populations will oust other species, including puffins, from their habitual nesting sites and force them into marginal locations or displace them altogether (Belopol'skii 1957, Tuck 1961, Williams 1974).

Intraspecific competition can also prevent potential breeders from obtaining a nest site, as exemplified in Rowan's (1965) account of Great Shearwaters (*Puffinus gravis*) on Nightingale Island, where as many as 200,000-300,000 eggs per year were deposited on the ground by birds unable to secure burrows. Alcids, such as puffins, are also territorial, defending only a small area, and site holders can exclude other birds from breeding (Nettleship 1972, Manuwal 1974a, Harris 1984, Birkhead 1985). The range of habitats a species is adapted to nest in, the types of sites available at a

specific location, and the presence of competing species interact to limit a bird's choice of nesting site.

1.2.2.3. Other costs

Other potential costs to nesting in colonies include conspicuousness to predators, competition for mates, kleptoparasitism, physical interference, cuckoldry, likelihood of misdirected parental care, intraspecific brood parasitism, intraspecific killing of young, and transmission of ectoparasites or disease (Hoogland and Sherman 1976, Birkhead 1985, Wittenberger and Hunt 1985).

The relative importance of various costs and benefits to colonial nesting will differ among species and depend on the mixture of species interacting at a particular location. Selective action of these factors will help differentiate high quality from low quality sites within a colony.

1.2.3. Factors affecting intra-colony variation in breeding success

1.2.3.1. Site characteristics

Within colonies, nest site quality and the habitat choices birds make are affected by social and environmental factors (Klopfer and Hailman 1965, Rowan 1965, Buckley and Buckley 1980, Burger and Shisler 1980, Potts et al. 1980, Kharitonov and Seigel-Causey 1988, Podolsky and Kress 1989). Higher quality sites provide protection against environmental stresses (Dexheimer and Southern 1974,

Montevecchi 1978, Potts et al. 1980, Burger and Gochfeld 1987, Harris and Wanless 1988, Storey et al. 1988, Clark et al. 1990, Seddon and van Heezik 1991, Stokes and Boersma 1991, Thompson and Furness 1991, Aebischer 1993, Chastel et al. 1993), reduce risks of predation and kleptoparasitism (Cullen 1957, Nettleship 1972, Birkhead 1977, Montevecchi 1977, Galbraith 1983, Ewins and Tasker 1985, Emms and Verbeek 1989, Anderson and Hodum 1993), limit intraspecific harassment, predation and cannibalism (Davis and Dunn 1976, Parsons 1976, Montevecchi and Wells 1984, Reville 1991, Schaffner 1991), and satisfy requirements of physiological and behavioural adaptations for nesting (Nelson 1978, Gaston and Nettleship 1981, Birkhead et al. 1985). If limited, high quality nest sites are a valuable commodity and individuals possessing them expend energy to defend and maintain them, forcing some individuals to nest in marginal locations or not at all (Rowan 1965, Manuwal 1974a, Birkhead 1978, 1985, Harris 1984, Greenwood 1987, Nelson 1987, Harris and Wanless 1989, 1990, Hatch 1989). When the quality of a site is defined by its physical characteristics, its location is stable and changes only as environmental conditions change. When a site's quality depends on social factors, its location is relative and changes as social structures change within and between seasons. The interaction of physical and social factors makes it difficult to define nest site quality independently of breeding success at any particular site (but see Potts et al. 1980).

We can infer that seabirds exhibit preferences in their selection of nest sites from the sequence in which birds use different types of sites during seasonal re-occupation of a colony and during colony formation and expansion (Burger and Shisler 1980, Pierotti 1982, Coulson and Thomas 1985, Storey and Lien 1985, Jehl and Mahoney 1987, Porter and Coulson 1987, Kharitonov and Seigel-Causey 1988). The density of nests found in different habitats also can reflect habitat preferences (Manuwal 1974b, Vermeer 1979, Harris 1980, Watanuki 1985, Schramm 1986, Wilson and Manuwal 1986, Sklepkovych and Montevecchi 1989), unless density is constrained by physical characteristics of the habitat which limit the availability of nest sites or other resources required for nesting (Hilden 1965).

1.2.3.2. Nesting density

Many studies have found correlations between nesting density and breeding success. For alcid species such as puffins or murres, positive correlations between nesting density and breeding success are associated with high risks of predation (Nettleship 1972, Birkhead 1977, Harris 1980, Hatchwell 1991) and are absent where predation is minimal (Ashcroft 1979, Harris and Wanless 1988). Dense groups gain protection from predators through predator swamping, increased synchrony, and defensive behaviour. In contrast, reproductive success is often unrelated or negatively correlated with nesting density in gull species due to intra-specific aggression and predation (Vermeer 1963, Patterson 1965, Davis and Dunn

1976, Parsons 1976, Pierotti 1987, Pierroti and Murphy 1987, Spaans et al. 1987, Bukacinska and Bukacinska 1993). For such species, the costs of territoriality can be equal to or greater than the benefits accrued by defending a site in a preferred habitat. Alcids have behavioural adaptations for high density nesting which minimize costs of defending a nest site (Birkhead 1978, 1985, Taylor 1984). Benefits of enhanced predator defence minus low costs of territoriality may result in net benefits for alcids nesting at high density.

1.2.3.3. Timing and synchrony

Breeding synchrony and timing have been correlated with nesting density in several studies (Birkhead 1977, Montevecchi et al. 1979, Burger and Shisler 1980, Gochfeld 1980, Hatchwell 1991), although some studies have found no relationship between them (Vermeer 1963, Harris and Wanless 1988). Breeding success is often correlated with timing and thus indirectly with nest density, although benefits vary depending on the kinds of predation or other pressures operating on individuals at a particular colony. Early breeders are often more successful than late breeders (Grant 1971, Nettleship 1972, Davis and Dunn 1976, Manuwal 1979, Birkhead and Nettleship 1981, Gaston and Nettleship 1981, Ryder and Ryder 1981, Pierotti 1982, Boersma and Ryder 1983, Coulson and Thomas 1985, Harris and Birkhead 1985, Shaw 1986, McNeil and Leger 1987, Ollason and Dunnet 1988, Wanless and Harris 1988, Mills 1989, Hatchwell 1991, Harris et al. 1992, Smith and Carlile 1992).

Selective effects of predation on early or late breeders can result in highest success rates for pairs nesting at peak periods (Kruuk 1964, Patterson 1965, Nisbet 1975, Hunt and Hunt 1976, Parsons 1975). Relationships between timing of breeding and success also can depend on, and be modified by, temporal patterns and changes in food availability (Emlen and Demong 1975, Hatch 1990, Regehr 1994).

1.2.3.4. Age and experience

The influence of age and experience on timing of breeding and success has been repeatedly demonstrated in seabirds (Ollason and Dunnet 1978, 1986, 1988, Lloyd 1979, Haymes and Blokpoel 1980, Hunt 1980, Ryder 1980, Coulson and Thomas 1985, Nelson 1988, Reid 1988, Wooller et al. 1988, 1989, 1990, 1992, Bradley et al. 1991, Hamer and Furness 1991, Croxall et al. 1992, Emslie et al. 1992, Pugesek and Wood 1992, Weimerskirch 1992, Aebischer 1993) and can offset effects of habitat or location because older, more experienced birds do better regardless of where they nest (Nelson 1978, 1988, Ainley et al. 1983, Coulson 1988, Thomas and Coulson 1988, Meathrel et al. 1993). Site tenacity also increases with age and successful breeding (Coulson and Dixon 1979, Coulson and Thomas 1980, Harris 1984, Hudson 1985, Gaston 1992), suggesting that familiarity and skills gained by successfully breeding at one site constitute fitness benefits that outweigh potential benefits and costs of moving to alternative, possibly better sites. Breeding success is often higher in the centre than on the edge of a colony or group due to the relative

distribution of experienced and inexperienced birds (Coulson 1968, 1988, Nelson 1978, Coulson and Dixon 1979, Ainley et al. 1983, Coulson and Thomas 1985, Porter and Coulson 1987, Thomas and Coulson 1988), although differential effects of predation are also important (Paterson 1965, Tenaza 1971, Dexheimer and Southern 1974, Montevecchi 1978, Reid 1988).

1.2.3.5. Colony formation

An important consideration relevant to habitat studies is the fact that the age and spatial structure of a colony is not fixed but changes from year to year and during a single season (Johnson 1941, Burger and Shisler 1980, Kharitonov and Seigel-Causey 1988, Aebischer and Wanless 1992, King et al. 1992, Murphy et al. 1992, Williams and Rodwell 1992). The seasonal ontogeny of a colony affects its structure and the relative success of birds nesting in different sections. Experienced breeders generally return first, forming nuclei around which the colony or subgroups within the colony grow (Burger and Shisler 1980, Kharitonov and Seigel-Causey 1988). New breeders recruit more frequently into peripheral areas, and much of the difference in breeding success between central and peripheral nesters can be explained by differences in age and breeding experience (Nelson 1978, 1988, Ainley et al. 1983, Coulson 1988), although when high quality nest sites are limited, the possession of a good site can also affect success. The strong site tenacity exhibited by most seabird species, as well as the fact that young, unsuccessful or divorced

breeders tend to change nest sites more frequently than older, successful pairs affects the dynamics of colony formation and the resultant colony structure (Gaston and Nettleship 1981, Hatch 1987, Ollason and Dunnet 1988). The fluidity of colony structure is especially apparent during periods of expanding or declining populations and when population demography is changing (Davis 1975). When a colony is contracting, peripheral nesters may be the oldest, most successful individuals remaining in a formerly densely occupied area. This may explain the situation on Dun where puffins nesting in sparse areas were on average older than those in dense parts of the colony (Harris 1980).

1.3. Puffins on Great Island

Atlantic Puffins, like other members of the Alcidae, have compactly shaped bodies with short wings adapted for wing-propelled, underwater pursuit of prey. For nesting they typically excavate burrows in the soil in which they incubate a single egg and feed their chick until fledging. Prey brought to nestlings is mostly fish and is carried conspicuously, held crosswise in the bill. Chicks make their own way to sea when they are capable of flight, usually fledging during the night to reduce risks of predation (Lockley 1953, Harris 1984).

In this study I investigate the distribution of puffins within their largest breeding colony in the western Atlantic (Nettleship and Evans 1985). Populations breeding on Great Island have probably increased this century following reduction

of human exploitation, although Nettleship suspected a decrease of 25 to 35% between 1969 and 1979 due to fisheries impacts on capelin (*Mallotus villosus*), puffins' primary summer prey (Brown and Nettleship 1984, Nettleship and Evans 1985, Nettleship 1991). Estimates of declining populations were based on changes in numbers of burrows counted in a limited sample area and may not represent the entire colony (Cairns and Verspoor 1980).

Great Island is an appropriate study site because habitats are easily distinguished and previous work has documented differences in breeding success and nesting density in different habitats (Nettleship 1972). Puffins nesting in slope habitat had higher breeding success than those in level habitat, and body mass of males was larger in slope than in level habitat (Nettleship 1972). Burrow density was also higher in slope habitat (Nettleship 1972), and the effects of habitat and density may have been confounded (Harris 1984). Density in one study area on Great Island was explained primarily by distance from the cliff edge (part $r^2 = 0.66$) plus soil depth (part $r^2 = 0.12$), and only minimally, though significantly, by angle of slope (part $r^2 = 0.03$) (Nettleship 1972). Breeding success as well as density may have been more related to distance from shore than slope because level habitat occurred farther from shore than slope habitat. Harris (1980) also found that breeding success was higher and males tended to be larger in dense than in sparse nesting areas on Dun. Differences between dense and sparse areas on Dun were not related to slope.

Nettleship (1972) attributed differences in breeding success in slope and level habitats to higher egg and chick predation and kleptoparasitism by Herring Gulls (*Larus argentatus*) on level habitat. He hypothesized that higher egg mortality resulted from puffins on level habitat flushing more frequently from their burrows during panic flights initiated by gull alarm cries, displacing eggs towards the burrow entrance where gulls could obtain them. Chick mortality was explained by two factors: chicks on level habitat were fed less frequently, and hungry, experimental chicks spent more time near burrow entrances where they were vulnerable to gull predation than well-fed chicks. Adults returning with fish were robbed more frequently by kleptoparasitic gulls on level than on slope habitat, probably because they have difficulty taking off from level ground (Nettleship 1972). Predation on adult puffins was not considered by Nettleship although Great Black-backed Gulls (*Larus marinus*), a major predator at other colonies (Harris 1980, 1984), also breed on Great Island.

Although not investigated on Great Island, weather and soil drainage affect timing of breeding and quality of nest sites in different locations within a puffin colony (Hornung and Harris 1976, Harris 1980, 1984). In arctic and sub-arctic colonies such as Great Island, southern exposures, where the soil thaws earlier in the spring, and areas that are better drained are better nesting sites than colder, poorly drained sites (Hornung and Harris 1976, Harris 1984).

Inclement weather and commercial fishing may lower puffin breeding success on Great Island and elsewhere by reducing the availability of capelin or other important prey species (Nettleship 1972, 1991, Lid 1981, Brown and Nettleship 1984, Barrett et al. 1987). Recently, colder sea surface temperatures appear to have changed the availability of prey for nesting seabirds (Montevecchi and Myers 1992), resulting in high variability in reproductive success among species and at different colonies in Newfoundland (Montevecchi et al. 1992, Neuman 1994, Regehr 1994). Adverse environmental conditions can accentuate differences in reproductive performance of experienced and inexperienced breeders and favourable conditions may minimize those differences (Hatch 1990, Murphy et al. 1992). Periods of increased stress should result in greater differences in reproductive success between experienced and inexperienced breeders and between preferred and marginal habitats, facilitating tests of habitat selection models.

1.4. Previous applications of habitat selection theory to breeding seabirds

To my knowledge, theoretical models have been considered in only one study of a colonial-breeding seabird (Pierotti 1982). Similar breeding success for Herring Gulls nesting at different densities found in that study offered superficial agreement with predictions of an ideal-free distribution (Pierotti 1982). However, because Herring Gulls are territorial, distribution would not have been "free", and similar success across habitats probably resulted from a balance of costs and benefits for

unequal, despotic competitors (see Pierotti and Annett 1994) rather than a free distribution of equal competitors (see Parker and Sutherland 1986).

Although not addressed in other studies, it is useful to consider which habitat selection models best account for documented patterns in breeding performance of puffins on Great Island. Within some alcid colonies, consistent differences in breeding success between areas or habitats (Nettleship 1972, Harris 1984) and positive correlations between breeding density and success (Birkhead 1977, Harris 1980, Hatchwell and Birkhead 1991) agree with predictions of an ideal-despotic model (Fretwell and Lucas 1970). Higher breeding success and burrow density in slope than in level habitat found by Nettleship (1972) for puffins on Great Island is a good example. The fact that puffins are territorial also fits the premise of that model. However, larger males in slope habitat suggests that birds are assorted according to differences in competitive ability. As well, distance from the edge of the colony, soil depth, soil drainage, slope, and aspect, have been shown to be important factors influencing breeding success, density, and timing of nesting puffins. These factors probably interact at a variety of spatial scales within a colony, creating differences in nest site quality both within and between habitat categories (e.g., slope and level). Thus, from what we know about puffins in general and on Great Island, the distribution of puffins nesting on Great Island may be best explained by some blend of ideal despotic (Fretwell and Lucas 1970), phenotype-limited ideal free (Parker and Sutherland 1986), and ideal preemptive (Pulliam and Danielson 1991)

models. My goal will be to distill this eclectic mixture into a manageable form. Bear in mind that all these models assume that average fitness within a habitat declines with increasing consumer density. This assumption remains to be evaluated.

1.5. Aims and predictions

My purpose is to determine whether current habitat selection models can explain the distribution of puffins on Great Island, and, if not, to propose a model that can. Field studies were conducted to: 1) determine if differences between slope and level habitats found by Nettleship (1972) persist through time; 2) separate effects of slope and distance from the edge of the colony by determining which physical variables discriminate habitats for puffins; 3) determine the relationship between burrow density and breeding success within and between habitats; 4) determine whether density can be used as a measure of habitat preferences; and 5) evaluate the relative importance of differences due to variation in individual competitive ability or nest site quality and differences due to broader habitat characteristics. I approached the field studies with certain predictions in mind based on the results of previous studies, known weather patterns at Great Island, and anticipating reduction in the availability of food for puffins because of cold sea surface temperatures. This allowed me to answer specific questions required to meet my objective. My predictions were:

1) The most important habitat variables that discriminate habitat quality for puffins on Great Island are distance from the shore edge of the colony, slope, and aspect. Breeding success and density will be highest close to shore, on steeper slopes, and at south or west facing aspects. Aspect may be important to breeding puffins for two reasons: insolation creates more favourable thermal environments at south than north aspects, and prevailing wind direction creates better flight conditions on windward than on leeward aspects. Wind may also affect thermal environments at Great Island because cold winds are from the north and east and warm winds are from the south and west (Atmospheric Environment Service, St. John's). Prevailing winds were westerly during the 1992 and 1993 breeding seasons (Atmospheric Environment Service, St. John's). If insolation is the dominant factor, timing and breeding success should follow a south-north gradient, whereas if prevailing wind direction is most important, they should follow a west-east gradient.

2) Burrow density will be related to the same habitat variables that contribute to breeding success and will reflect habitat preferences.

3) Timing of breeding is constrained by when burrows thaw and dry in the spring and so will be related to habitat variables in the order: aspect, slope, and distance from the shore edge of the colony.

4) Previous studies have shown that risks of predation and kleptoparasitism are greater where density is low and on level ground so I predict that breeding success

will be related to habitat variables in the order: distance from the edge, slope, and aspect.

5) More birds will lay eggs and hatch and fledge chicks in slope habitat than in level habitat, and on south and west sides than on north and east sides of the island.

6) Due to the higher energy demands of brooding and provisioning chicks than laying and incubating eggs (Ricklefs 1983), I predict that greater differences in reproductive performance between slope and level habitats and between south and north locations will occur during the nestling period than the incubation period.

To test these predictions, I investigated the variability in breeding performance of Atlantic Puffins nesting in different habitats and locations on Great Island in 1992 and 1993. I used the two habitats, maritime slope and maritime level, identified by Nettleship (1972) plus a third, inland slope, identified by Cairns and Verspoor (1980). Including inland slopes, which tended to be farther from shore than level habitat, helped to distinguish effects due to slope and distance. I sampled birds nesting on the north, east, south and west sides of the island. I assumed that there was a greater proportion of experienced breeders in 'optimal', slope or south and west areas than in 'marginal', level or north and east areas, and I would not be able to separate effects of age or experience from those related to position or habitat. I expected that birds nesting in inland slope habitat should exhibit intermediate success due to the interaction of nesting on slope and being farther from shore than those in maritime level habitat.

I used proportions of burrows that interconnected as a measure of interference among burrowing puffins to help evaluate the prediction that burrow density reflects habitat preferences. It is possible that burrow density is unrelated to habitat preferences and is simply a function of topography and the volume of soil available for burrowing (Harris 1984, Harris and Birkhead 1985). If this was the case, I would expect that the frequency with which birds were digging into each other's burrows would be similar across densities. Alternatively, if density is related to habitat preferences, then interference should be higher at higher densities.

I compared variation within and between areas to assess the relative contributions of individual and habitat differences and to evaluate habitat selection models that assume equal competitive ability among individuals. I used breeding success as a measure of fitness that incorporates both individual and habitat components. This was acceptable because the components are complementary, i.e., individuals with higher fitness should occur in preferred habitats, and I need only a relative measure of habitat quality. Relationships between success in 1992 and 1993 were analyzed to help determine the importance of individual fitness. Birds that successfully fledged chicks in 1992 were expected to be more successful in 1993 than birds that failed in 1992. Success per burrow was used as a representative measure of individual success, assuming that most birds retained 1992 nest sites in 1993.

Causes of egg and chick mortality were assessed to evaluate previous explanations for observed differences in breeding success between slope and level habitats. Rates of chick growth, feeding, and kleptoparasitism were measured in this study and will be reported elsewhere (Rodway unpubl.).

Chapter 2

METHODS

2.1. Study site

Great Island (47°11'N 52°46'W) is part of the Witless Bay Ecological Reserve and lies approximately 2.4 km off the southeast shore of the Avalon Peninsula in southeast insular Newfoundland (Fig. 2). The island is about 1200 m long and ranges from about 150 to 700 m wide. Eastward tilting of underlying strata results in topography on Great Island aligned north to south with most slopes facing east and west, some facing north, and few facing south. Steep, grassy slopes above a precipitous, rocky shoreline change to level or gently sloping, perimeter grassy areas, *Rubus*-grass meadows, and a central forested area. North-south running ridges create steep interior slopes covered with forest or grass. The island has been described in detail by Nettleship (1972). Forested area has contracted and perimeter grassy and meadow habitats have expanded since the time of Nettleship's study (J. Reddick, Bauline East, NF, pers. comm.). Changes are especially obvious on the southern end and along the east and north sides of the island where dead snags are abundant. The activities of nesting birds, particularly puffins and Herring Gulls, have probably contributed to habitat changes (Harris 1984). Nine seabird species are known to breed on the island, including an estimated 52,000 pairs of Atlantic Puffins, 2,770 pairs of Herring Gulls, and 80 pairs of Great Backed-backed Gulls (Cairns et al.

1989). Puffins nest in grassy, perimeter areas with enough soil to support burrows and on inland slopes as far as 200 m from shore.

2.2. Sampling methods

The study was conducted from 20 May to 28 August with three subsequent visits on 31 August, 7 September and 26 September in 1992, and from 4 June to 30 August with an additional visit on 6 September in 1993. The population sampled, and to which I wished to make inferences, was the nesting population of puffins on Great Island. A stratified, centered start, systematic sampling scheme (Madow and Madow 1944, Madow 1949, 1953) was used to insure adequate representation of different parts of the colony. The scheme was designed *a priori*, before the colony had been visited, and was considered unbiased. Samples were stratified by habitat and location. I defined level habitat the same as Nettleship ($< 15^{o}$), but changed the criteria for slope habitat (from $> 30^{o}$ to $> 15^{o}$) in order to include the entire colony in the sampling population. This angle was appropriate to distinguish habitats because, with no wind, puffins have difficulty taking flight from slopes $< 15^{o}$ but not from steeper slopes (pers. obs.). The extent of different habitats was measured along transects laid out east to west every 100 m across the island (Fig. 2). Transects were marked every 5 m and sample plots were placed at 30 m intervals, or at the closest 5 m mark that fell within a particular habitat.

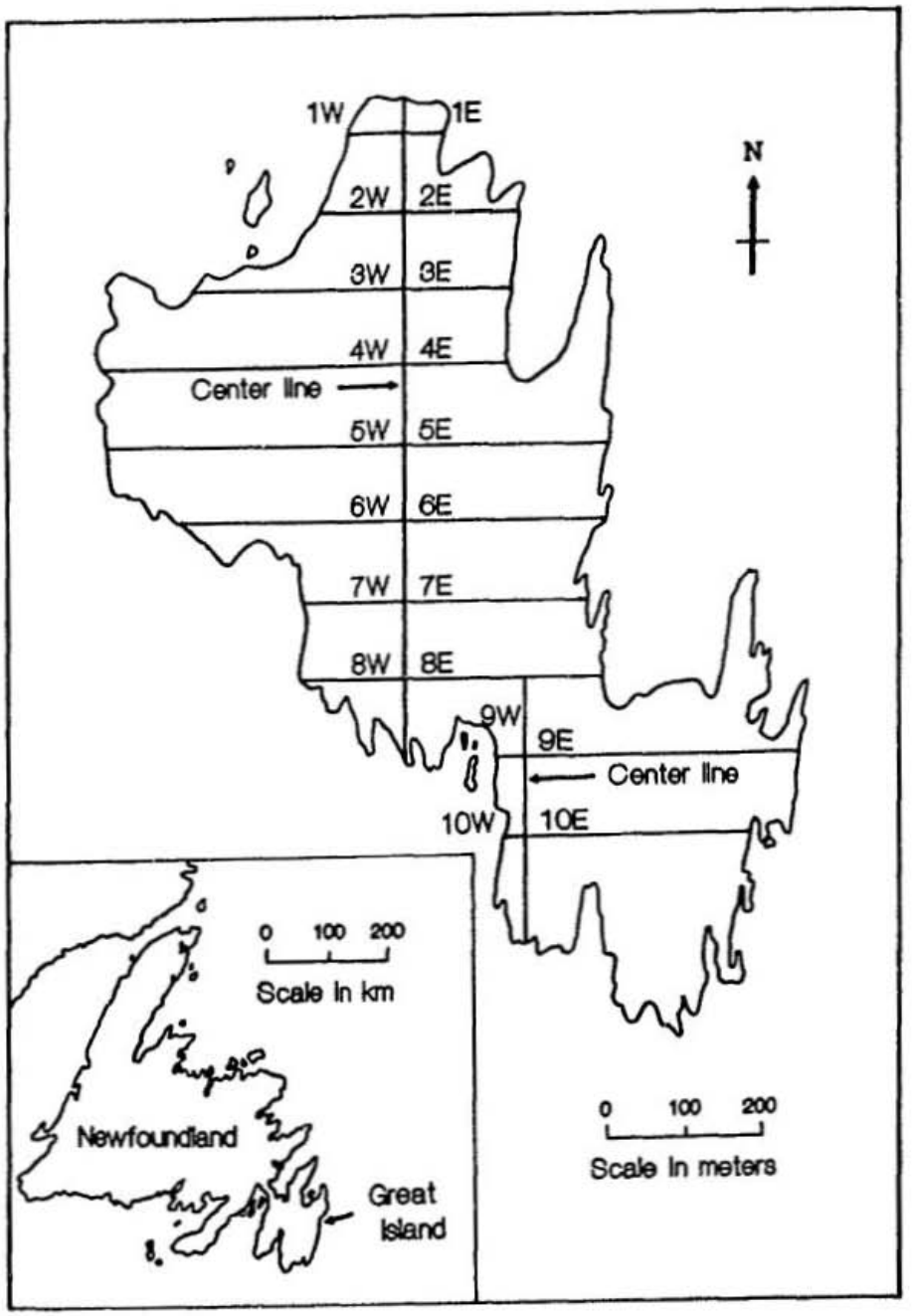


FIGURE 2. Location of transects used to distribute sample plots on Great Island in 1992 and 1993.

In 1992, three plots containing 20 burrows each were established for each habitat type and grouped by location on the north, east and south sides of the island. I was unable to include the west side of the island because it was impractical to walk there on a regular basis. The sample of burrows in each plot was obtained by selecting all burrows occurring within contiguous 1 m^2 sections, until 20 burrows were identified. Sections were examined in a predetermined sequence in an expanding radius from a measured point along a transect. This selection technique avoided potential biases caused by choosing burrows that looked occupied or were easier to access. Standard criteria were used to define a burrow. An entrance was called a burrow if its tunnel extended more than 50 cm and did not connect with another entrance within 100 cm. If it did connect with another entrance within 100 cm, the two (or more) entrances were called a single burrow. In rare cases, tunnels less than 50 cm were called burrows if they contained obvious nest cups, eggs or chicks.

Puffins are extremely sensitive to disturbance and will readily desert their nests (Lockley 1934, Harris 1984). To minimize disturbance, in 1992 burrows were checked once during incubation to determine if an egg had been laid, then every four days from just before hatching until near fledging, when the interval was shortened to two days to obtain fledging dates. If burrows were longer than an arm's reach, access hatches were dug on the first visit until either an egg was found or the burrow was verified as empty. Chicks were measured on each visit during the

nestling period (Rodway unpubl.). Ashcroft (1979) found that this visiting regime caused no reduction in productivity when compared to undisturbed controls. I established control plots of 20 burrows adjacent to each study plot. Those burrows were checked late in the nestling period and were followed to fledging to provide comparisons for productivity and timing. Breeding success in study plots was measured by the proportions of eggs laid, chicks hatched, and chicks fledged per burrow, and by the proportions of chicks hatched per egg laid (hatching success), chicks fledged per chick hatched (fledging success), and chicks fledged per egg laid (breeding success). Chicks fledged per burrow was compared between study and control plots.

In 1993, because of the effects of disturbance in 1992 (see Results), burrows in both study and control plots were first checked late in the nestling period. An additional sample of 195 burrows was distributed along the same transects measured in 1992, again stratified by habitat and location. I placed new plots on the north, east, and west sides and not on the south side of the island in 1993 because much of the remaining colony area at the south end of the island that was not sampled in 1992 was fragile peat that was easily eroded. Those burrows were checked once during incubation to determine if an egg had been laid, and once near the end of the nestling period to estimate breeding success. Fledging rates in 1993 were estimated by subtracting the percent mortality observed in 1992 for similar sized chicks from the total number of chicks observed in plots when they were checked in 1993. This

technique assumed that chick mortality near the end of the nestling period was similar in the two years, and may introduce a bias if feeding conditions differed between years. However, any bias would likely be small because many chicks were already near fledging when burrows were checked in 1993, and mainly small, late-hatched chicks died after this date in 1992.

Timing of hatching and fledging in 1993 were determined in a feeding observation plot (Rodway unpubl.) established in maritime level habitat on the south side of the island. All-day feeding watches were conducted every four days throughout the nestling period, and two-hour watches during the peak feeding period in the morning were conducted every second day during the hatching period. Chicks were assumed to be one day old when I observed the first feed delivered to the burrow (Harris 1984). When chicks approached fledging age (Nettleship 1972, Harris 1984, Rodway unpubl.), burrows were checked at one to two day intervals to determine actual fledging dates.

2.3. Habitat variables and burrow characteristics

For each plot I measured slope, aspect, and closest distance to the edge of puffin colony along the shore (hereafter referred to as "distance from edge"). Habitat measurements were taken when plots were first checked during June of 1992 and 1993. Because the edge of the colony did not always correspond to the edge of the vegetation, I defined the edge of the colony to be at the first puffin burrow

encountered, when moving from the shore towards the interior, within a 5 m perpendicular distance either side of a measurement line. Distance from edge was measured along the ground, thus including surface contours, to the nearest 0.1 m using a 30 m tape. Measurements were taken to the edge of the colony at shore even if sections of unused habitat intervened (e.g., some nesting areas on inland slopes were separated from colony along the shore by stretches of meadow or forest habitat which were not currently being used by puffins for nesting). Slope was measured to the nearest degree using a Silva Ranger compass and a protractor aligned with a plumb. Aspect was estimated to the nearest degree by sighting directly down slope with the compass.

Burrow characteristics were recorded: burrow length to the nearest 0.1 m, numbers of connecting entrances for burrows in main study plots, burrow density for each plot, temperatures of empty burrows in or near most study plots, and nest chambers categorized as wet or dry in all burrows that held eggs in study plots in 1992. Burrow density at each plot was determined by counting the number of burrows in a 4x4 m area or in the area used to obtain the 20 sample burrows, whichever was larger. Empty burrow temperatures were measured on 6-10 June 1993 in or near study plots at north, east, and south location (N = 54) and on 27 August 1993 in study plots at east and south locations (N = 12). Temperatures were taken at a distance of about 50 cm into a burrow with a Yellow Springs Instrument flexible thermo probe (series 400). Measurements were taken in the afternoon on

cloudy days to reduce potential biases caused by daily changes in temperature. A nest was categorized as wet if standing water was ever recorded in the nest during the period I was checking burrows to determine hatching dates and measure chicks.

2.4. Analyses

2.4.1. Categorical variables

Confirmatory analyses were performed on the effects of categorical explanatory variables (e.g., location and habitat) on continuous response variables (e.g., burrow density). Specific comparisons to test predictions (e.g., that burrow density will be higher at south and west locations than at north and east locations) were analyzed as planned comparisons using contrast matrixes (Wilkinson 1990). However, planned comparisons among group means were not always appropriate because some of my questions required non-orthogonal contrasts (Hays 1988). In those cases, effects were first tested using ANOVA followed by Tukey HSD post-hoc tests.

Logit models were used to analyze dichotomous measures of breeding success (e.g., egg laid or not laid) in relation to year, type of plot, location, and habitat categories. Logit-model analysis is a special application of hierarchical, log-linear models. It provides an ANOVA-like, confirmatory analysis for asymmetrical inquiry of cross-classified, categorical data, where one of the variables is defined as a response variable (Fienberg 1977, Kennedy 1983). In this case, response variables

are the dichotomous measures of breeding success, egg laid or not laid, chick hatched or not hatched, etc. These types of models are appropriate for analyzing count data where the response variables are poisson (Norusis 1990). The saturated logit-model (Kennedy 1983) in an example with eggs laid (or not laid) per burrow (E with i levels = 1,2) as the response variable and location (L with j levels = 1,3) and habitat (H with k levels = 1,3) as explanatory variables is given by,

$$\ln F_{ijk} = u + \lambda_i E_i + \lambda_j L_j + \lambda_k H_k + \lambda_{ij} E_i{*}L_j + \lambda_{ik} E_i{*}H_k + \lambda_{jk} L_j{*}H_k + \lambda_{ijk} E_i{*}L_j{*}H_k + \ln \epsilon_{ijk},$$

where F_{ijk} is the observed frequency in cell (i,j,k), u is the general effect equal to the average of the logs of the frequencies in all cells, $\lambda_i E_i$ is the effect of eggs laid, $\lambda_j L_j$ is the effect of location, $\lambda_k H_k$ is the effect of habitat, $\lambda_{ij} E_i{*}L_j$, $\lambda_{ik} E_i{*}H_k$, $\lambda_{jk} L_j{*}H_k$ and $\lambda_{ijk} E_i{*}L_j{*}H_k$ are effects due to first- and second-order interactions, and ϵ_{ijk} is the error equal to the difference between observed and expected frequencies in cell (i,j,k). Lambda parameters were estimated from fitting the model, and represent increments or decrements from the general level u for particular combinations of levels of the different variables (Norusis 1990). For example,

$$\lambda_j = u_j - u,$$

where u_j is the effect of being in column j.

In logit-model analysis, only interactions involving the response variables are of interest. 'Main effects' of explanatory variables are given by the interaction term of that variable with the response variable (Kennedy 1988). Higher order interactions can be interpreted in a fashion similar to interactions in multi-way ANOVAs (Elliot 1988). A 'null-logit model' can be defined that includes all first-order terms for individual variables plus all interaction terms that do not include the response variable (Kennedy 1988). The null-logit model for eggs laid per burrow is given by,

$$\ln F_{ijk} = u + \lambda_i E_i + \lambda_j L_j + \lambda_k H_k + \lambda_{jk} L_j{*}H_k + \ln \epsilon_{ijk}.$$

Null hypotheses of no effects due to explanatory variables were tested by evaluating the goodness-of-fit of null-logit models. If null-logit models fit observed data, then evidence was not present to reject null hypotheses in favour of alternate hypotheses. Specific alternative hypotheses were tested by comparing goodness-of-fit estimates of null-logit models with those of models that include 'main effects' or higher interactions involving the response variable (Kennedy 1988). The model to test the effects of location is given by,

$$\ln F_{ijk} = u + \lambda_i E_i + \lambda_j L_j + \lambda_k H_k + \lambda_{jk} L_j{*}H_k + \lambda_{ij} E_i{*}L_j + \ln \epsilon_{ijk}.$$

Predicted models for eggs laid, chicks hatched and chicks fledged in study burrows take similar forms,

$$\ln F_{ijk} = u + \lambda_i X_i + \lambda_j L_j + \lambda_k H_k + \lambda_{jk} L_j{*}H_k + \lambda_{ij} X_i{*}L_j + \lambda_{ik} X_i{*}H_k + \ln \epsilon_{ijk},$$

where X_i represents levels of one of those response variables. That is, for the model that best fits the data, the expected frequency in cell (i,j,k) is best accounted for by adding the effects of the interactions of the particular response variable with location and with habitat to the null-logit model. The second-order interaction effects of the response variable by location and habitat were not expected to be important. All logit models contained the terms from the null logit model in order to control for irrelevant, potentially contaminating differences in cell frequencies due to factors that do not involve the response variable (Kennedy 1983). Estimates of lambda parameters were used to evaluate the importance of the different levels of each explanatory variable. Null hypotheses of no differences in particular levels were tested with z-tests. Null hypotheses were rejected at the 5% level if $z > 1.96$ (Norusis 1990). Since lambdas sum to zero across levels of each variable, one test was required for interactions between dichotomous response and explanatory variables and 2 tests were required for interactions between dichotomous response and trichotomous explanatory variables. Thus, the number of z-tests required corresponded to the degrees of freedom for the term being evaluated. A per

comparison alpha rate of 5% was accepted because contrasts were based on a priori questions and because the number of tests did not exceed available degrees of freedom (for a similar justification in relation to error rates for planned, orthogonal comparisons in ANOVA models see Hays 1988).

Likelihood ratio tests (G^2), comparing observed and expected frequencies, were used to test hypotheses (Hays 1988). Likelihood ratio chi-squares were used in preference to Pearsonian chi-squares because of their additive properties and resultant usefulness for comparing component chi-squares in trying to determine the most parsimonious model that fits the data (Kennedy 1983). Tests for individual terms were given by the change in G^2 between two models that differed only by the inclusion or exclusion of that term. Terms were added in a predetermined, hierarchical sequence: Type of plot (where appropriate), Location, then Habitat, because I wished to test the effects of Habitat after Location and Type of plot had been considered (see Hays 1988 for a discussion of an hierarchical approach to testing hypotheses using linear regression models). Partial components were also inspected and lead to similar conclusions as hierarchical components. This indicated that there was little correlation among explanatory variables and the order of entry into the model did not affect changes in goodness-of-fit estimates due to particular variables.

The criterion for rejection of null hypotheses was a goodness-of-fit estimate for the null-logit model with a probability of less than 5% when compared to the

theoretical chi-square distribution. A tolerance level of 5% for Type I error was also used to test hypotheses for individual effects. Using the theoretical chi-square distribution for tests was considered acceptable if at least 80% of expected cell frequencies were greater than five (Hays 1988). If low cell frequencies were a problem, tables were collapsed by habitat and by location, to give two condensed tables with adequate cell frequencies. Results from the collapsed and original tables were compared. Likelihood ratio chi-squares and Pearsonian chi-square were also compared, which, if they lead to the same conclusions, gave some assurance that sample sizes were adequate to evaluate the chosen model (Clogg and Eliason 1987).

The same types of diagnostics for residuals used in regression analysis can be used in logit-model analysis. If a model adequately fits the data, standardized residuals should be independent, normally distributed and within limits of $\pm$ 1.96 (Norusis 1990). Normal plots of standardized residuals and plots of standardized residuals against observed and expected frequencies were examined for normality and independence from the model. Tables of standardized residuals were inspected for outliers. Residuals from all analyses were deemed acceptable. Logit-model and residual analyses were conducted using SPSS* (Norusis 1990) and SYSTAT (Wilkinson 1990) statistical packages.

2.4.2. Continuous variables

Null hypotheses of no effects due to continuous, habitat variables were tested using multiple linear regression. Aspect had to be transformed from a circular scale to a linear scale to be included in linear models. This was accomplished by assigning minimum (0) and maximum (180) values to opposite directions and giving symmetrical values increasing from 0 to 180 to each hemisphere. Because compass directions are arbitrary, this was done four different ways, assigning 0 at north, northeast, east, and southeast directions. To test hypotheses involving aspect, the directional scale which best approximated a linear relationship with the dependent variable being tested was entered into the regression model.

Variance within and between plots for each measure of breeding success was partitioned using ANOVA. This required no special assumptions as long as inferences to the population were not attempted (Hays 1988). Mean values per plot (e.g., mean number of eggs laid per burrow in each plot) were used to provide continuous response variables and meet assumptions for regression models testing predicted relationships between measures of breeding success and habitat variables. Using mean values means that variation within plots was not considered and that reported proportions of variance accounted for by habitat variables did not include within-plot differences.

As with log-linear models, terms were entered into a model in a predetermined, hierarchical sequence to determine the contributions of individual

predictor variables (Hays 1988). Tolerance for Type I error was set at 5%. Residuals were inspected to insure that assumptions of normality and homoscedasticity were satisfied. Means are quoted $\pm$ 1 SD unless otherwise stated.

Chapter 3

RESULTS

3.1. Burrow characteristics

3.1.1. Burrow density

Burrow density in study plots varied from 0.16 to 2.00 burrows/m^2. Mean density was higher at south (0.96 $\pm$ 0.29 burrows/m^2; N = 6) and west (1.31 $\pm$ 0.50 burrows/m^2; N = 15) locations than at north (0.87 $\pm$ 0.56 burrows/m^2; N = 14) and east (0.71 $\pm$ 0.25 burrows/m^2; N = 11) locations (planned comparison: $F_{1,14} = 5.70$, P = 0.023). Results of 2-way ANOVA indicated significant effects due to habitat ($F_{2,34} = 5.38$, P = 0.009) and the interaction of habitat by location ($F_{6,14} = 2.77$, P = 0.026; Fig. 3). Across habitats, mean burrow density ranged from a high of 1.20 $\pm$ 0.52 burrows/m^2 in maritime slope (N = 19), to 0.92 $\pm$ 0.45 burrows/m^2 in maritime level (N = 15), and a low of 0.74 $\pm$ 0.41 burrows/m^2 in inland slope (N = 12) habitat. Differences between maritime slope and inland slope were significant (Tukey: P = 0.009). The effect of habitat varied across locations, differing most between north and east locations (Fig. 3).

Distance from edge, slope, and aspect were expected to be important explanatory variables for burrow density. This model explained 31% of the variation in burrow density and supported effects by distance from edge and aspect (Table 1).

Exploration of density data revealed that the relationship between burrow density and distance from edge was better described by a log function than a linear

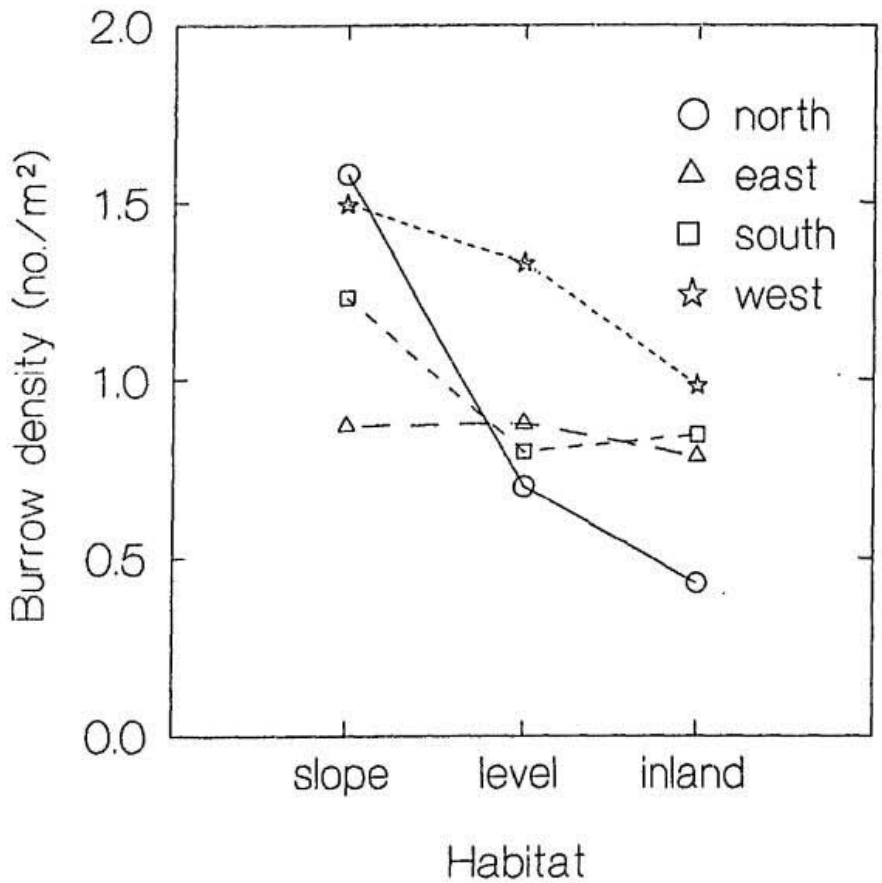


FIGURE 3. Interaction of habitat and location for density of Atlantic Puffin burrows on Great Island.

TABLE 1. ANOVA summary for multiple regression of density of Atlantic Puffin burrows on Great Island on distance from the shore edge of the colony, slope, and aspect. Variables were added hierarchically in the order listed.

Source	r^2	Standard coefficient	Mean square	df	F	P
Predicted linear model						
Distance	0.20	-0.441	2.189	1	11.83	0.001
Slope	0.00	0.057	0.034	1	0.18	0.674
Aspect[a]	0.11	0.340	1.257	1	6.79	0.013
Full model	0.31		1.160	3	6.28	0.001
Residual			0.185	42		
Non-linear model						
Log distance	0.35		3.966	1	24.63	0.000
Piecewise slope[b]	0.05		0.175	3	1.09	0.366
Aspect	0.03		0.293	1	1.82	0.185
Full model	0.43		0.957	5	5.94	0.001
Residual			0.161	40		

[a] Aspect coded from southeast = 0 to northwest = 180; see Methods.

[b] Breakpoint for piecewise regression was at 27 °.

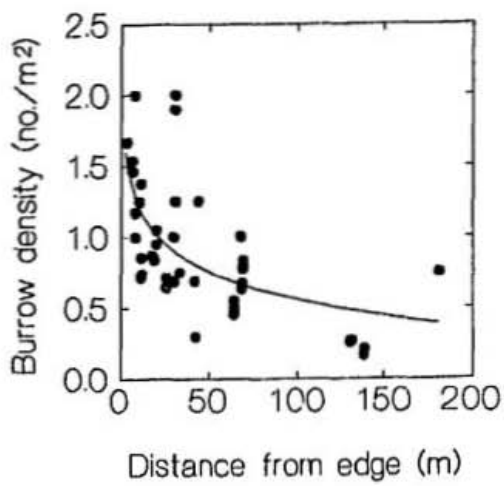
function (Fig. 4). A plot of density against slope showed that burrow density peaked at slopes between 20 and 30 ° and the relationship was best fitted with a piecewise linear regression line (Wilkinson 1990). Using the log of distance and a piecewise term for slope in the predicted model significantly increased explained variance from 31 to 43% ($F_{2,40}$ = 8.10, P = 0.001) and indicated that distance from edge, but not slope or aspect, was a good predictor of burrow density (Table 1).

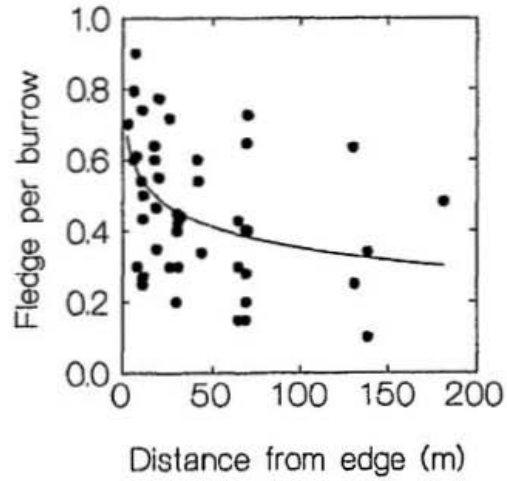
The effects of habitat and distance were confounded because the three habitats were at consistently different distances from the shore edge of the colony. To separate these effects I tested the relationship between density and distance from edge within each habitat. The relationship between density and log distance held within maritime slope (r^2 = 0.29, $F_{1,17}$ = 6.97, P = 0.017) and maritime level (r^2 = 0.51, $F_{1,13}$ = 13.80, P = 0.003) habitats, but I was unable to reject a null hypothesis of no effect due to distance for inland slope habitat (r^2 = 0.01, $F_{1,10}$ = 0.07, P = 0.797).

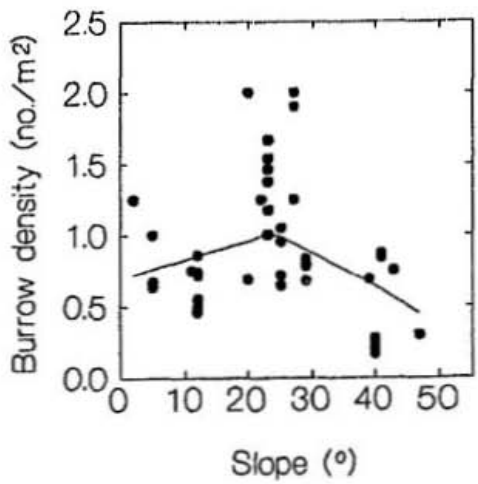
3.1.2. Burrow length and interference

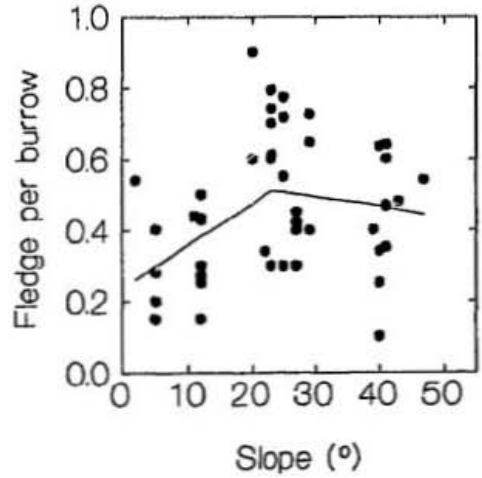
Burrow length ranged from 20 to 280 cm and differed by location ($F_{3,550}$ = 6.29, P < 0.0001) and habitat ($F_{2,550}$ = 15.03, P < 0.0001). Mean burrow length was greater at south (83 $\pm$ 25 cm; N = 123) than at north (75 $\pm$ 20 cm; N = 203; Tukey pairwise comparison: P = 0.011), east (76 $\pm$ 27 cm; N = 166; Tukey: P = 0.025), and west (68 $\pm$ 16 cm; N = 70; Tukey: P < 0.001) locations. Maritime

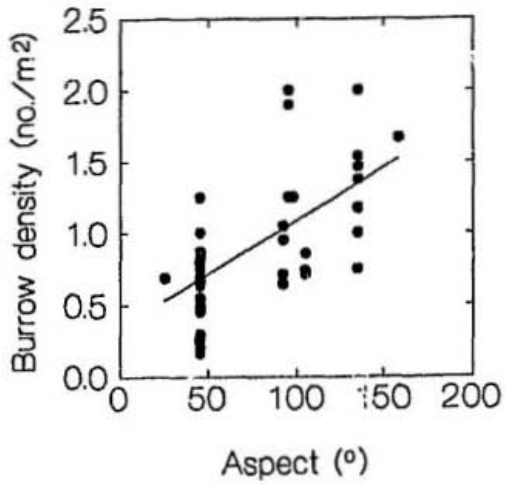
FIGURE 4. Comparison of burrow density and mean number of chicks fledged per burrow in relation to distance from the shore edge of the colony, slope, and aspect for Atlantic Puffins nesting on Great Island in 1992 and 1993.

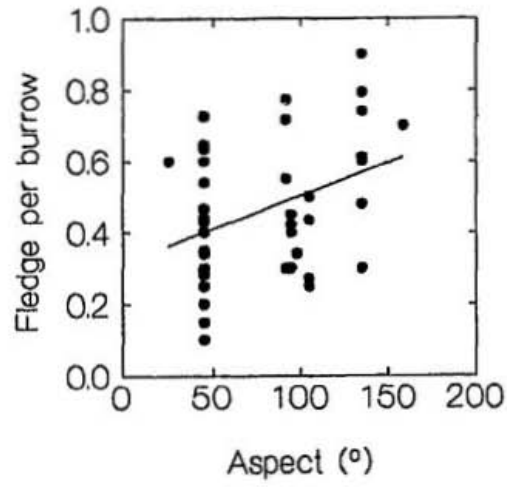

Burrow density (no./m2)
2.5
2.0
1.5
1.0
0.5
0.0
0
50
100
150
200
Distance from edge (m)


Fledge per burrow
1.0
0.8
0.6
0.4
0.2
0.0
0
50
100
150
200
Distance from edge (m)


Burrow density (no./m2)
2.5
2.0
1.5
1.0
0.5
0.0
0
10
20
30
40
50
Slope (°)


Fledge per burrow
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
Slope (°)


Burrow density (no./m2)
2.5
2.0
1.5
1.0
0.5
0.0
0
50
100
150
200
Aspect (°)


Fledge per burrow
1.0
0.8
0.6
0.4
0.2
0.0
0
50
100
150
200
Aspect (°)

level habitat had longer burrows (86 ± 31 cm; N = 187) than inland (74 ± 17 cm; N = 167; Tukey: P < 0.001) and maritime (69 ± 16 cm; N = 208; Tukey: P < 0.001) slope habitats. Proportions of burrows with interconnecting entrances were higher on maritime slope (38%; N = 120) than on maritime level (18%; N = 120; X^2_1 = 12.04, P = 0.0005) and inland slope (18%; N = 120; X^2_1 = 10.95, P = 0.0009) habitats. I could detect no difference across locations in the proportions of burrows with interconnecting entrances (X^2_2 = 2.73, P = 0.255).

Mean burrow length per plot declined with increasing burrow density (r^2 = 0.12, $F_{1,44}$ = 5.91, P = 0.019; Fig. 5), and numbers of interconnecting entrances in main study plots increased with density (r^2 = 0.49, $F_{1,16}$ = 15.20, P = 0.001; Fig. 5).

3.1.3. Burrow temperature

When I first visited Great Island on 9 May 1992, many burrows, especially on north facing slopes, were blocked with ice. Burrow temperatures in the second week of June 1993 varied from 4.0 to 10.2 °C and differed by location ($F_{2,51}$ = 4.19, P = 0.021) and not by habitat ($F_{2,51}$ = 1.13, P = 0.332). Mean temperatures were 7.3 ± 1.5 °C at south (N = 20), 5.9 ± 1.1 °C at east (N = 10), and 7.0 ± 0.9 °C at north (N = 24) locations. Differences were significant between south and east locations (Tukey pairwise comparison: P = 0.017). Samples paired by location on the north and east sides of the island showed that burrow temperatures averaged

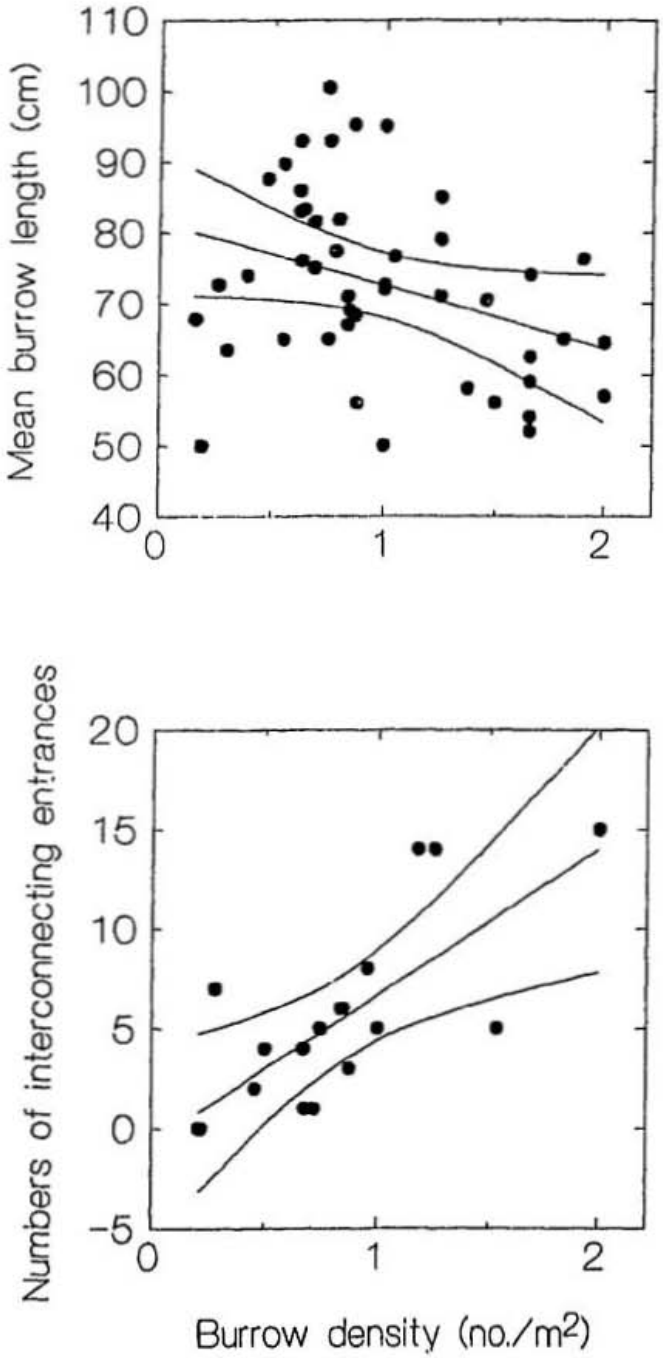


FIGURE 5. Comparison of mean burrow length and numbers of interconnecting entrances per plot in relation to burrow density. Linear regression lines are shown ± 95% confidence limits.

slightly higher in maritime slope (7.4 ± 0.8 ± °C; N = 11) than in maritime level (6.4 ± 0.9 °C; N = 17) habitat in the same area ($F_{1,26}$ = 9.10, P = 0.006). Burrow temperatures differed by aspect ($F_{3,49}$ = 7.74, P = 0.0003), and were higher on south facing slopes (8.3 ± 1.3 °C; N = 10) than on north (6.7 ± 1.4 °C; N = 17; Tukey: P = 0.002), east (6.7 ± 0.5 °C; N = 17; Tukey: P = 0.001) and west (6.2 ± 1.0 °C; N = 10; Tukey: P = 0.001) facing slopes.

Temperatures measured in a small sample of empty burrows on the east and south sides of the island on 27 August 1993 were slightly higher at south locations with west aspect (12.8 ± 0.9 °C; N = 6) than at east locations with east aspect (11.9 ± 0.4 °C; N = 6; $F_{1,10}$ = 5.56, P = 0.040).

3.1.4. Nest flooding

Rainfall in July 1992 recorded at St. John's (139.9 mm) was almost double the 30-year average (75.3 mm; Atmospheric Environment Service, St. John's). Most (97.8 mm) of the monthly total fell during the first 10 days of July when most puffin chicks were hatching (see Timing of breeding). Flooding in nest chambers was recorded in 35% of all burrows containing eggs. Many other burrows had wet tunnels but nests remained dry. Proportions of nests that flooded were similar at north (35%, N = 40), east (31%, N = 48), and south (39%, N = 49) locations (X^2_2 = 0.60, P = 0.740). Differences in the proportion of burrows that had wet nests in maritime slope (42%, N = 43), maritime level (38%, N = 48), and inland slope (26%, N =

46) habitats were not significant ($X^2_2 = 2.63$, $P = 0.269$). Burrows closer to the cliff edges in maritime slope and maritime level habitats received more runoff and seepage water in heavy rains.

The degree and duration of flooding differed among plots. Only plots in maritime slope and maritime level habitat at the south end of the island retained enough water to float eggs in nest chambers. Eggs were floating, some for more than a week, in six nests in the maritime slope plot and one nest in the maritime level plot during the second week of July. Wet burrows in other plots drained better and dried faster.

Rainfall was also above average in June (185.7 mm) and July (140.4 mm) 1993 (30-year average for June was 83.4 mm), most of which fell in the last week of June and first week of July (181.8 mm).

3.2. Timing of breeding

3.2.1. Hatching and estimated egg-laying dates

In 1992, mean hatching dates were 3-4 days earlier at south than at north and east locations (planned comparison: $F_{1,74} = 5.19$, $P = 0.026$; Table 2). Differences across habitats were not significant ($F_{2,71} = 2.06$, $P = 0.135$). Distributions of hatching dates were positively skewed and dispersion to the right was greater at east than at south locations ($X^2_1 = 3.91$, $P = 0.048$; Fig. 6; chi-square tests comparing locations, habitats, and years were performed on the proportion of chicks hatching

more than one week after median hatch dates). Distributions did not differ significantly between south and north locations ($X^2_1 = 0.48$, $P = 0.489$). Dispersion of hatching dates was greater in maritime slope and inland slope habitats than in maritime level habitat (Table 2, Fig. 7), though differences were significant only between level and maritime slope ($X^2_1 = 4.37$, $P = 0.037$) and not between level and inland slope ($X^2_1 = 3.69$, $P = 0.055$) habitats. Hatching dates in 1993 were similar to the overall average in 1992 (means: $F_{1,121} = 1.36$, $P = 0.246$, Table 2; distributions: $X^2_4 = 5.18$, $P = 0.270$, Fig. 8). Subtracting an incubation period of 42 days (Nettleship 1972, Harris 1984) from hatching dates gives estimated median egg-laying dates of 26 and 27 May in 1992 and 1993, respectively.

Results of ANOVA of hatching date by plot revealed that 88% of the variance in hatching dates was within plots. Thus, habitat variables, that primarily distinguished plots, were not expected to account for a large proportion of the variance in hatching dates. Regression of date of hatching on burrow density showed no significant trend ($r^2 = 0.01$, $F_{1,74} = 0.41$, $P = 0.526$). The predicted model that included aspect, slope, and distance from edge accounted for a significant proportion of the variance in hatching dates (Table 3). Aspect made the only significant contribution to the fit of the model.

Analysis of the relationship between hatching date and aspect, slope, and distance from edge was repeated using mean hatching date per plot as the dependant value. This reduced sample size but eliminated the high variability within plots. The

TABLE 2. Timing of breeding of Atlantic Puffins on Great Island in 1992 and 1993.

	Hatching dates				Fledging dates							
					Study plots				Control plots			
	N	Median	Mean (S.E.)	Spread[a] (days)	N	Median	Mean (S.E.)	Spread (days)	N	Median	Mean (S.E.)	Spread (days)
1992												
By location												
North	19	7 Jul	8 Jul (1.1)	7	11	31 Aug	30 Aug (3.0)	22	19	17 Aug	21 Aug (2.4)	19
East	36	7 Jul	9 Jul (1.3)	17	19	30 Aug	1 Sep (3.0)	28	23	23 Aug	26 Aug (1.7)	22
South	21	4 Jul	5 Jul (0.7)	7	17	18 Aug	22 Aug (1.9)	20	33	20 Aug	22 Aug (1.3)	18
By habitat												
Maritime slope	26	6 Jul	8 Jul (1.2)	13	19	25 Aug	29 Aug (2.8)	29	32	22 Aug	24 Aug (1.5)	25
Maritime level	22	7 Jul	6 Jul (0.8)	9	12	23 Aug	25 Aug (2.5)	21	19	21 Aug	21 Aug (1.9)	17
Inland slope	28	7 Jul	9 Jul (1.4)	17	16	21 Aug	26 Aug (3.1)	27	24	19 Aug	22 Aug (1.9)	23
All plots	76	7 Jul	8 Jul (0.7)	13	47	23 Aug	27 Aug (1.7)	32	75	20 Aug	23 Aug (1.0)	20
1993	47	8 Jul	9 Jul (1.1)	18	-	-	-	-	32	20 Aug	23 Aug (1.5)	24

[a] 10th to 90th percentile.

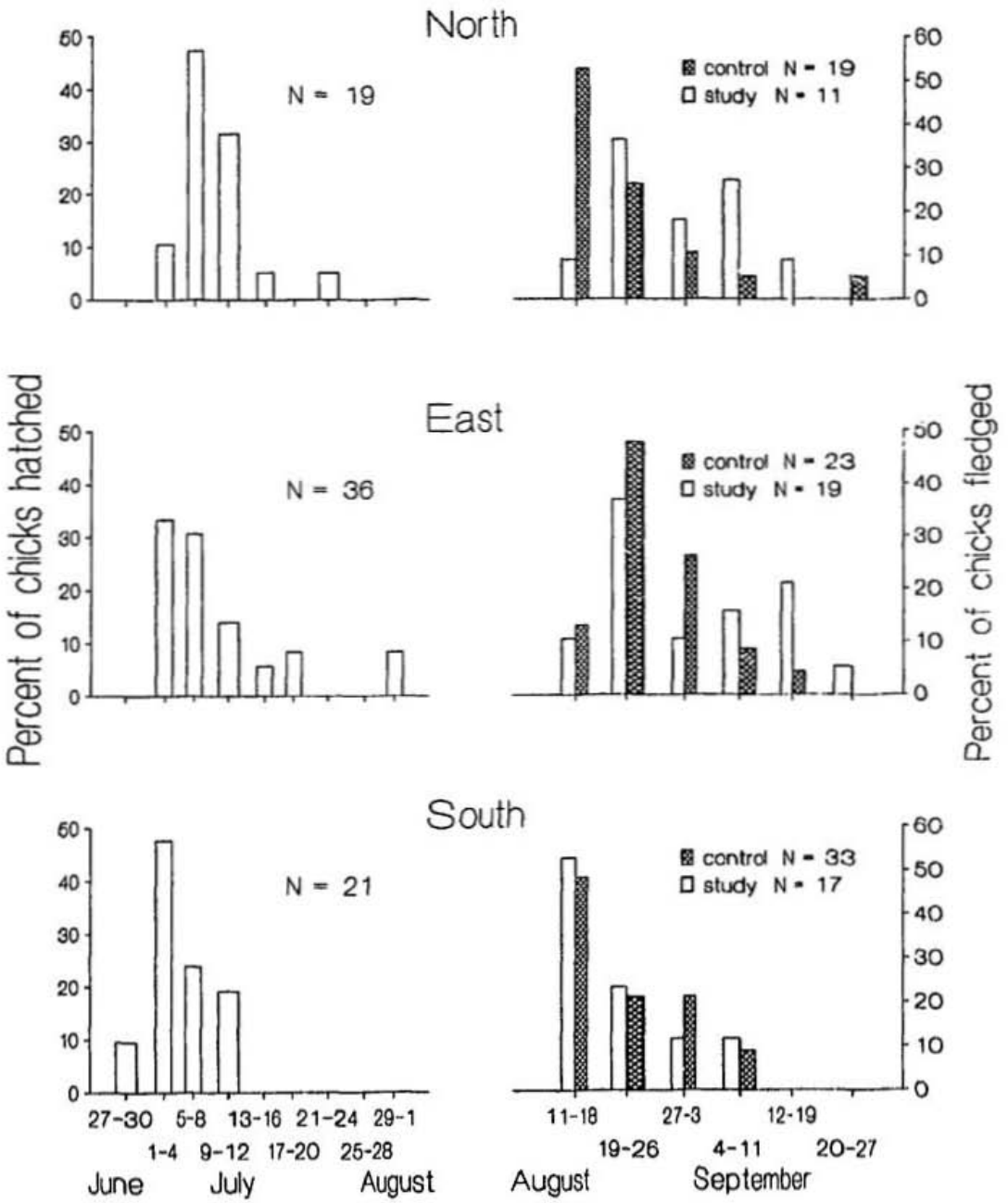


FIGURE 6. Distributions of hatching and fledging dates of Atlantic Puffins at different locations on Great Island in 1992.

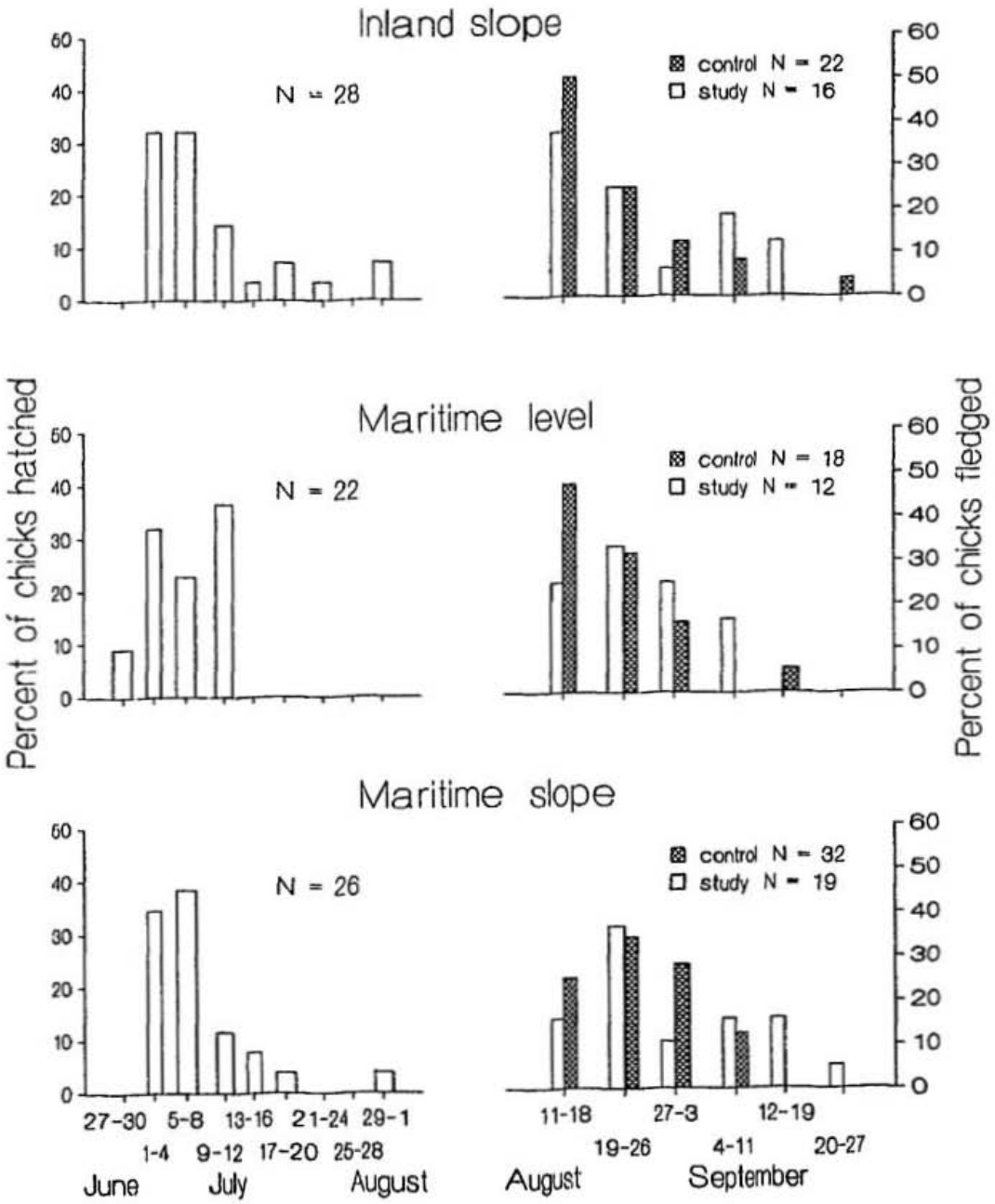


FIGURE 7. Distributions of hatching and fledging dates of Atlantic Puffins in different habitats on Great Island in 1992.

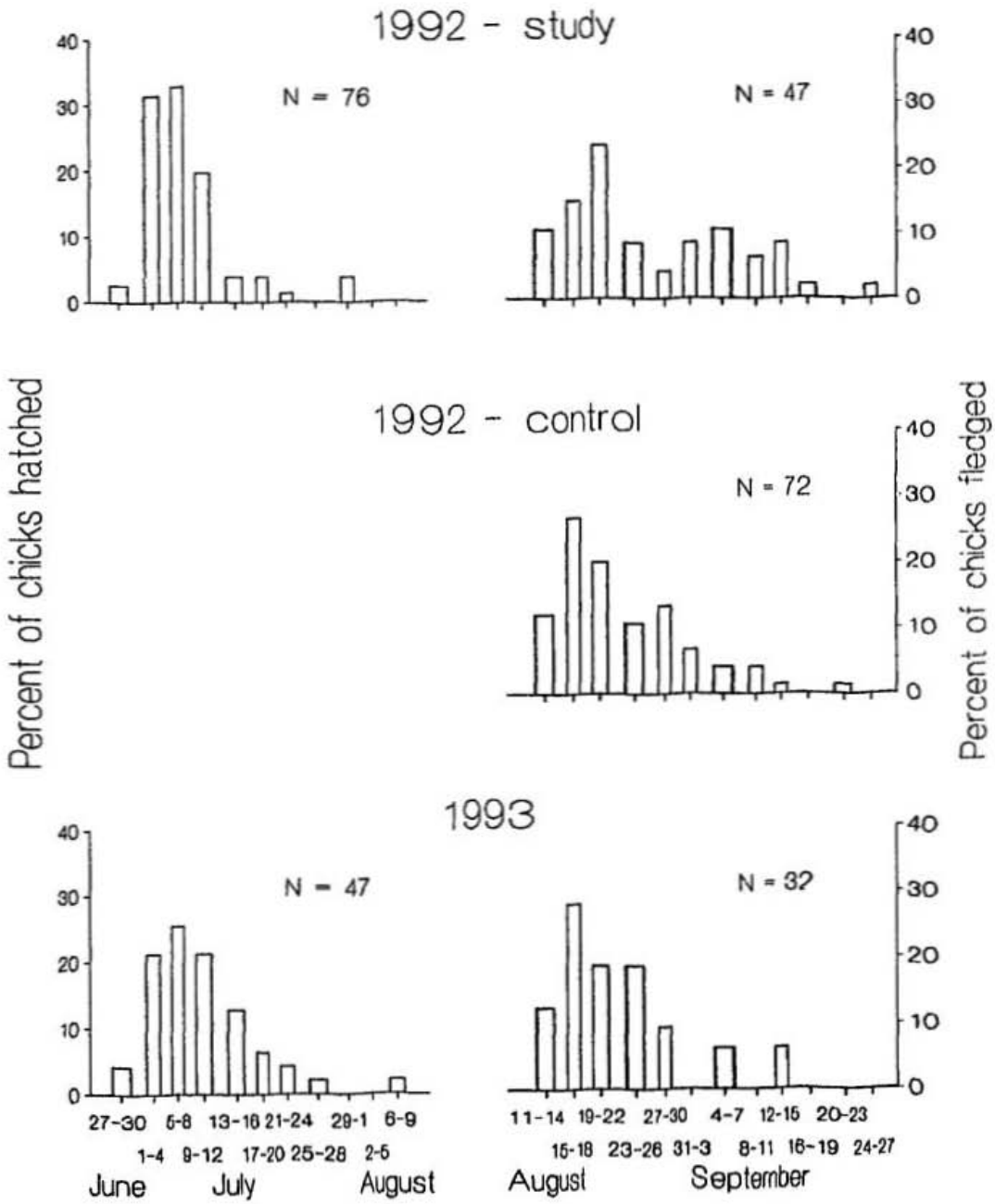


FIGURE 8. Distributions of hatching and fledging dates of Atlantic Puffins in study and control plots on Great Island in 1992 and 1993.

TABLE 3. ANOVA summary for multiple regressions of timing and synchrony of hatching dates of Atlantic Puffin chicks on Great Island in 1992 on aspect, slope, and distance from the shore edge of the colony. Variables were added hierarchically in the order listed.

Source	r^2	Standard coefficient	Mean square	df	F	P
Individual hatching dates						
Aspect[a]	0.07	-0.257	195.2	1	5.36	0.023
Slope	0.03	0.196	110.8	1	3.04	0.085
Distance	0.01	0.108	18.2	1	0.50	0.482
Full model	0.11		108.1	3	2.97	0.038
Residual			36.4	72		
Mean hatching dates per plot						
Aspect	0.58	-0.761	28.97	1	37.87	0.002
Slope	0.32	0.580	16.13	1	21.08	0.006
Distance	0.02	0.201	1.13	1	1.48	0.278
Full model	0.92		15.41	3	20.13	0.003
Residual			0.77	5		
Range of hatching dates per plot						
Aspect	0.37	-0.612	222.2	1	12.25	0.017
Slope	0.42	0.657	249.5	1	13.76	0.014
Distance	0.06	-0.315	31.7	1	1.75	0.244
Full model	0.85		167.8	3	9.25	0.017
Residual			18.1	5		

[a] Aspect coded from east = 0 to west = 180; see Methods.

predicted model accounted for 92% of the variance in mean hatching dates (Table 3). Aspect and slope made significant contributions to explained variance. The effect of slope was positive, hatching dates being later in steeper slopes (Table 3).

Aspect was analyzed separately to address the question of whether prevailing wind direction or insolation contributed most to timing of breeding. Aspect graded on an east-west basis accounted for 58% of the variance in mean hatching dates among plots ($F_{1,7}$ = 9.62, P = 0.017) compared to 18% accounted for by north-south coding ($F_{1,7}$ = 1.54, P = 0.254). Hatching tended to be earliest at west and latest at east aspects.

Apparent differences in synchrony between plots could be a spurious effect due to differences in the numbers of chicks hatched in those plots. Range of hatching dates within plots was not significantly correlated with the number of chicks hatched in a plot (r = 0.48, P = 0.188), indicating that other factors contributed to hatching synchrony. Aspect and slope accounted for a significant proportion of the variance among plots in the range of hatching dates (Table 3). As with timing of hatching, slope was positively related to the range of hatching dates. Range tended to be smaller in plots with westerly aspect than in plots with easterly aspects. Burrow density was not significantly related to the range of hatching dates (r^2 = 0.08, $F_{1,7}$ = 0.57, P = 0.476).

3.2.2. Fledging dates

Fledging was earlier ($F_{1,120}$ = 5.96, P = 0.016) and more synchronous (X^2_5 = 13.30, P = 0.021) in control plots than in study plots in 1992 (Table 2; Fig. 8). Differences between control and study plots were more pronounced at north and east and not apparent at south locations (Table 2; Fig. 6). This indicated that the effect of disturbance varied at different locations. To test this idea, I calculated the difference between mean fledging dates in study and control plots for each paired sample (Table 4). Results of ANOVA showed no significant effect of location on difference in mean fledging dates between study and control plots (r^2 = 0.32, $F_{2,6}$ = 1.40, P = 0.319). However, inspection of differences in paired plots (Table 4) revealed that the difference at plot 5E-70 was an exception to the general trend of greater differences between study and control at north and east than at south locations. If plot 5E-70 is excluded from the analysis, results of ANOVA support the hypothesis that the effect of disturbance was more pronounced at north and east than at south locations (r^2 = 0.72, $F_{2,5}$ = 6.33, P = 0.043). Excluding plot 5E-70 may be justified because only two, early-hatching chicks survived to fledging out of 12 eggs laid in the study plot at 5E-70. Thus, the effects of disturbance may have been severe at that plot but did not result in later fledging dates because all later chicks died or did not hatch (see below). The effect of disturbance did not vary significantly across habitats, whether plot 5E-70 was excluded (r^2 = 0.01, $F_{2,5}$ = 0.03, P = 0.972) or not (r^2 = 0.06, $F_{2,6}$ = 0.20, P = 0.821). Fledging dates in 1993 did not differ

significantly from those in control plots in 1992 (means: $F_{1,105} = 0.02$, $P = 0.902$; Table 2; distributions: $X^2_4 = 3.85$, $P = 0.427$; Fig. 8).

Earlier hatching at south than north and east locations may have been responsible for the differential effects of disturbance across locations noted above. Nests at which chicks hatched later would have received more visits during incubation, and thus more disturbance to incubating adults, than nests where chicks hatched earlier. I recorded whether an egg was warm or cold and whether an adult was encountered on each visit to a burrow. The number of visits on which a warm egg was found was greater at north (2.2 $\pm$ 0.2 visits) than at east (1.8 $\pm$ 0.2 visits) and south (1.3 $\pm$ 0.2 visits) locations ($F_{2,126} = 5.35$, $P = 0.006$). The same was true for the number of times an incubating adult was encountered (1.9 $\pm$ 0.2 at north, 1.3 $\pm$ 0.2 at east, and 1.0 $\pm$ 0.1 at south locations; $F_{2,134} = 10.18$, $P < 0.0001$).

Chicks at south locations fledged earlier, on average, than chicks at north and east locations ($F_{2,116} = 4.48$, $P = 0.013$ after effects due to Type of plot had been considered; Table 2, Fig. 6). I was unable to detect an effect of habitat on fledging date ($F_{2,116} = 1.01$, $P = 0.367$; Fig. 7). Differences in distributions of fledging dates among locations and habitats in study and control plots (Table 1; Fig. 6 and 7) were not significant ($X^2_2 < 1.8$, $P > 0.4$ for all comparisons). Greater variation in fledging than hatching dates ($F_{46,75} = 3.32$, $P < 0.0001$) made it more difficult to detect trends.

TABLE 4. Differences between mean fledging dates of Atlantic Puffin chicks in study and control burrows for each set of paired plots on Great Island in 1992.

Plot	Location	Habitat	Mean fledging date [days after 30 June (N)] Study	Control	Difference (days)
2E-120	North	Maritime slope	63.3 (6)	51.8 (8)	11.5
2E-85	North	Maritime level	60.3 (3)	51.3 (6)	9.0
5E-70	North	Inland slope	52.0 (2)	54.6 (5)	-2.6
5E-280	East	Maritime slope	66.6 (7)	58.6 (12)	8.0
5E-230	East	Maritime level	58.8 (4)	57.5 (3)	1.3
7E-220	East	Inland slope	60.9 (8)	51.9 (8)	9.0
10E-5	South	Maritime slope	51.2 (6)	54.4 (12)	-3.2
9W-20	South	Maritime level	52.0 (5)	49.6 (10)	2.4
9E-95	South	Inland slope	54.3 (6)	53.9 (11)	0.4

Type of plot was included as a dummy variable (Hays 1988) in regression models relating timing of fledging to burrow density and to distance from edge, slope, and aspect, in order to control for the observed difference in timing between study and control plots in 1992. Burrow density was not related to date of fledging (partial $r^2 = 0.00$, $F_{1,119} = 0.01$, $P = 0.915$). The predicted model including the three habitat variables accounted for 14% of the variation in fledging dates (Table 5). Proportion of variance within plots was 77%. If mean fledging date per plot was used as the dependant measure, the predicted model accounted for 68% of the variation between plots, with aspect again making the only significant contribution after the effect of type of plot had been accounted for (Table 5). As with hatching dates, fledging tended to be earlier at west than east aspects.

Ranges of fledging dates were similar in study and control plots ($r^2 = 0.01$, $F_{1,16} = 0.09$, $P = 0.765$) and type of plot was not included in regression models. Weak correlation between numbers of chicks fledged in a plot and range of fledging dates ($r = 0.27$, $P = 0.271$) again indicated that other factors influenced synchrony. Burrow density was not significantly related to range of fledging dates ($r^2 = 0.02$, $F_{1,15} = 0.03$, $P = 0.861$). Slope accounted for a significant proportion of the variance in range of fledging dates among plots (Table 5). The effect of the overall model including aspect, slope, and distance from edge failed to reach significance (Table 5). A better model would include only the effect of slope ($r^2 = 0.34$, $F_{1,15} = 7.79$, $P = 0.014$). As with hatching dates, the range of fledging dates tended

TABLE 5. ANOVA summary for multiple regressions of timing and synchrony of fledging dates of Atlantic Puffin chicks on Great Island in 1992 on type of plot, aspect, slope, and distance from the shore edge of the colony. Variables were added hierarchically in the order listed.

Source	r^2	Standard coefficient	Mean square	df	F	P
Individual fledging dates						
Type of plot	0.05		579.6	1	6.40	0.013
Aspect[a]	0.05	-0.231	651.6	1	7.19	0.008
Slope	0.01	0.105	116.7	1	1.29	0.259
Distance	0.03	-0.214	306.5	1	3.38	0.068
Full model	0.14		413.6	4	4.56	0.002
Residual			90.6	117		
Mean fledging dates per plot						
Type of plot	0.25		93.2	1	9.27	0.010
Aspect	0.30	-0.547	111.4	1	11.09	0.006
Slope	0.07	0.262	24.9	1	2.48	0.141
Distance	0.06	-0.356	23.1	1	2.30	0.155
Full model	0.68		63.2	4	6.29	0.006
Residual			10.0	12		
Range of fledging dates per plot						
Aspect	0.07	-0.257	67.1	1	1.43	0.253
Slope	0.30	0.558	309.5	1	6.60	0.023
Distance	0.03	0.248	31.4	1	0.67	0.428
Full model	0.40		136.0	3	2.90	0.075
Residual			46.9	13		

[a] Aspect coded from east = 0 to west = 180; see Methods.

to be greater in steeper slopes.

3.3. Breeding success

3.3.1. Egg-laying

Eggs were laid in 76% of burrows in 1992 and 87% of burrows in 1993 (Tables 6 and 7). Differences between years were significant ($X^2_1 = 6.95$, $P = 0.008$), even if plots on the west side of the island, which was not sampled in 1992, were excluded ($X^2_1 = 6.21$, $P = 0.013$). In 1992, frequencies of eggs laid per burrow were lowest at the north end of the island and were similar across habitats (Table 6, Fig. 9). Proportions of burrows with eggs were similar across locations and were lowest in inland slope habitat in 1993 (Table 7). The null-logit model was the most parsimonious model fit to the data in both years (1992: $G^2_8 = 9.14$, $P = 0.331$; 1993: $G^2_8 = 9.77$, $P = 0.282$). There was no evidence to support interaction effects or main effects of location and habitat, although z-tests of lambda values approached significance for north location in 1992 ($z = -1.94$, $P = 0.052$) and were significant for inland slope habitat in 1993 ($z = -2.41$, $P = 0.016$).

Data from 1992 and 1993 were combined to increase sample size for tests of regression models for numbers of eggs laid per burrow. Year was included as a dummy variable to control for differences between years. Most (91%) of the variance in numbers of eggs laid per burrow was within plots. Differences between plots in the mean number of eggs laid per burrow were positively related to burrow density

TABLE 6. Breeding success of Atlantic Puffins on Great Island in 1992.

	Study plots						Control plots	
	No. eggs laid per burrow (N)	Hatching success (N)	No. eggs hatched per burrow (N)	Fledging success (N)	Breeding success (N)	No. chicks fledged per burrow (N)	No. chicks fledged per burrow (N)	Breeding success (N)[a]
By location								
North	0.67 (60)	0.48 (40)	0.32 (60)	0.58 (19)	0.28 (40)	0.18 (60)	0.32 (60)	0.48
East	0.80 (60)	0.75 (48)	0.60 (60)	0.53 (36)	0.40 (48)	0.32 (60)	0.38 (60)	0.48
South	0.82 (60)	0.43 (49)	0.35 (60)	0.81 (21)	0.35 (49)	0.28 (60)	0.55 (60)	0.67
By habitat								
Maritime slope	0.72 (60)	0.61 (43)	0.43 (60)	0.73 (26)	0.44 (43)	0.32 (60)	0.53 (60)	0.74
Maritime level	0.80 (60)	0.46 (48)	0.37 (60)	0.55 (22)	0.25 (48)	0.20 (60)	0.32 (60)	0.40
Inland slope	0.77 (60)	0.61 (46)	0.47 (60)	0.57 (28)	0.35 (46)	0.27 (60)	0.40 (60)	0.52
All plots	0.76 (180)	0.56 (137)	0.42 (180)	0.62 (76)	0.34 (137)	0.26 (180)	0.42 (180)	0.55

[a] Estimated assuming similar proportions of eggs laid in study and control plots.

TABLE 7. Breeding success of Atlantic Puffins on Great Island in 1993.

	No. eggs laid per burrow (N)[a]	Breeding success[a]	No. chicks fledged per burrow (N)			
			New plots in 1993	Study plots from 1992	Control plots from 1992	All plots combined
By location						
North	0.82 (45)	0.72 (37)	0.59 (45)	0.40 (57)	0.51 (66)	0.50 (168)
East	0.87 (45)	0.65 (39)	0.56 (45)	0.48 (62)	0.58 (60)	0.54 (167)
South	-	-	-	0.57 (60)	0.62 (64)	0.60 (124)
West	0.89 (105)	0.68 (93)	0.60 (105)	-	-	0.60 (105)
By habitat						
Maritime slope	0.89 (90)	0.73 (80)	0.65 (90)	0.50 (58)	0.63 (62)	0.60 (210)
Maritime level	0.92 (60)	0.63 (55)	0.58 (60)	0.39 (64)	0.37 (63)	0.44 (187)
Inland slope	0.76 (45)	0.65 (34)	0.49 (45)	0.58 (57)	0.71 (65)	0.61 (167)
All plots	0.87 (195)	0.68 (169)	0.59 (195)	0.49 (179)	0.57 (190)	0.55 (564)

[a] Determined only in new plots.

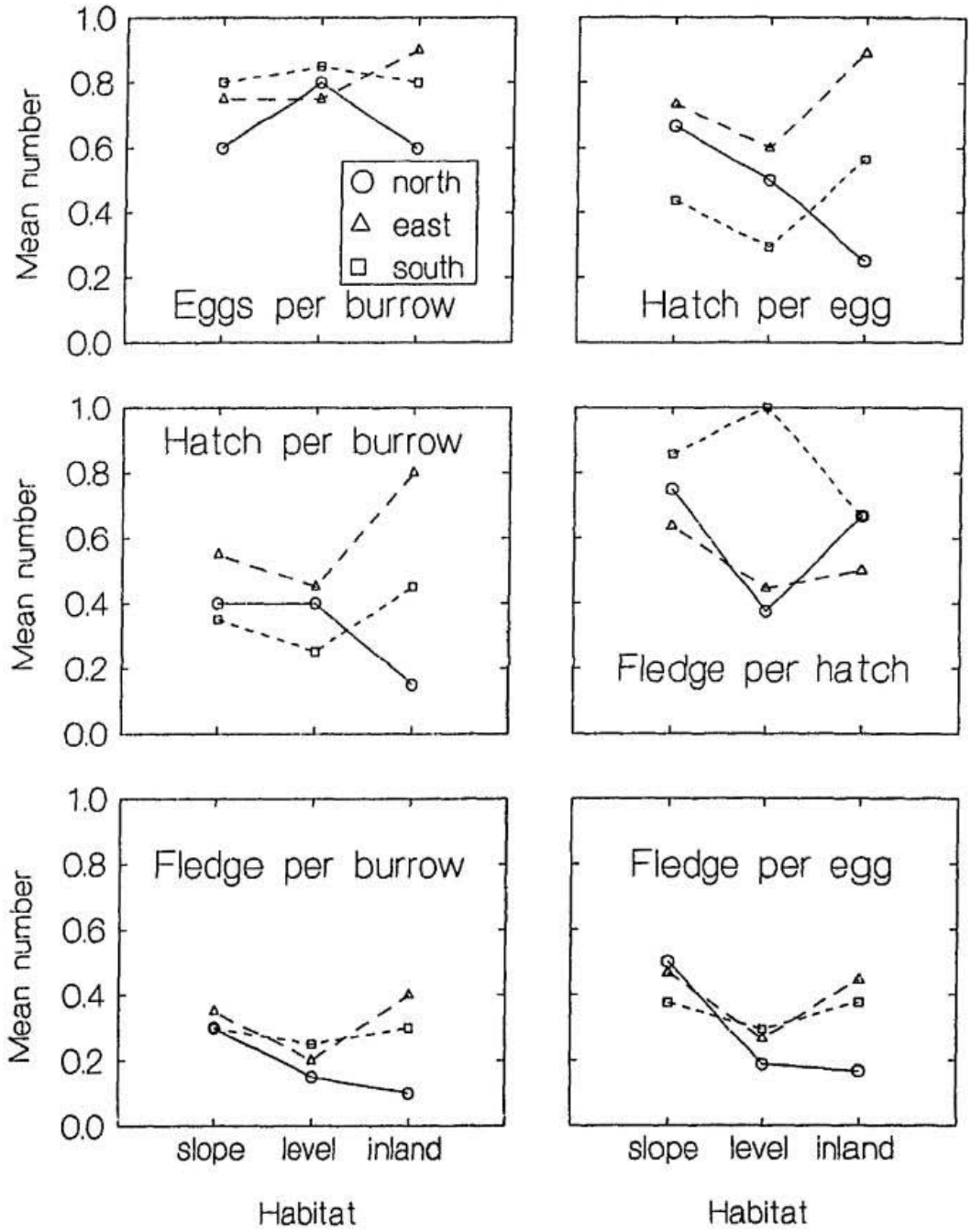


FIGURE 9. Interaction of habitat and location for measures of breeding success of Atlantic Puffins on Great Island in 1992.

(part $r^2 = 0.20$, $F_{1,17} = 5.04$, $P = 0.034$) after differences between years were considered. Eggs laid per burrow declined with increasing distance from the edge of the colony and, contrary to predictions, with increasing slope (Table 8). Aspect did not add significantly to explained variance.

3.3.2. Egg mortality

The majority of eggs that failed to hatch in 1992 were abandoned in the nest (Table 9, Fig. 10). Fifty-nine percent (N = 61) of those that did not hatch were abandoned or had disappeared by the first week in July when I began checks for hatching. Those burrows had been disturbed only once before that (Table 9). Proportions of remaining eggs that were abandoned after two disturbances to incubating adults (39%, N = 36) were less than that after three or more disturbances (58%, N = 19), but differences were not significant ($X^2_1 = 1.81$, $P = 0.178$). I suspected that digging access hatches on the first visit may have contributed to nest desertion, but hatching success did not differ in burrows that required access hatches (57%, N = 82) and those that did not (53%, N = 55; $X^2_1 = 0.28$, $P = 0.596$).

Most abandoned eggs were later removed by puffins cleaning out their burrows. There was also no evidence that puffins flush and kick eggs out of their burrow when disturbed. I never found a warm egg displaced from the nest chamber during my visits. Puffins standing around generally flushed at my approach, but incubating birds tended to stay in their burrow, and birds standing at the entrance

TABLE 8. ANOVA summary for multiple regressions of mean number of Atlantic Puffin eggs laid per burrow on Great Island in 1992 and 1993 on distance from the shore edge of the colony, slope, and aspect. Year was included as a dummy variable to control for differences between years. Variables were added hierarchically in the order listed.

Source	r^2	Standard coefficient	Mean square	df	F	P
Predicted linear model						
Year	0.10		0.029	1	3.22	0.094
Distance	0.20	-0.477	0.059	1	6.56	0.023
Slope	0.19	-0.453	0.058	1	6.44	0.024
Aspect[a]	0.07	0.329	0.021	1	2.33	0.149
Full model	0.56		0.042	4	4.51	0.015
Residual			0.009	14		

[a] Aspect coded from southeast = 0 to northwest = 180; see Methods.

TABLE 9. Fate of Atlantic Puffin eggs that failed to hatch in study plots in 1992.

Date	No. of prior visits	Abandoned	Gone	Total (%)
5-6 July	1	28	8	36 (59)
9-10 July	2	13	0	13 (21)
13-14 July	3	6	1	7 (11)
17-18 July	4	2	1	3 (5)
21-22 July	5	2	0	2 (3)
Total (%)		51 (84)	10 (16)	61 (100)

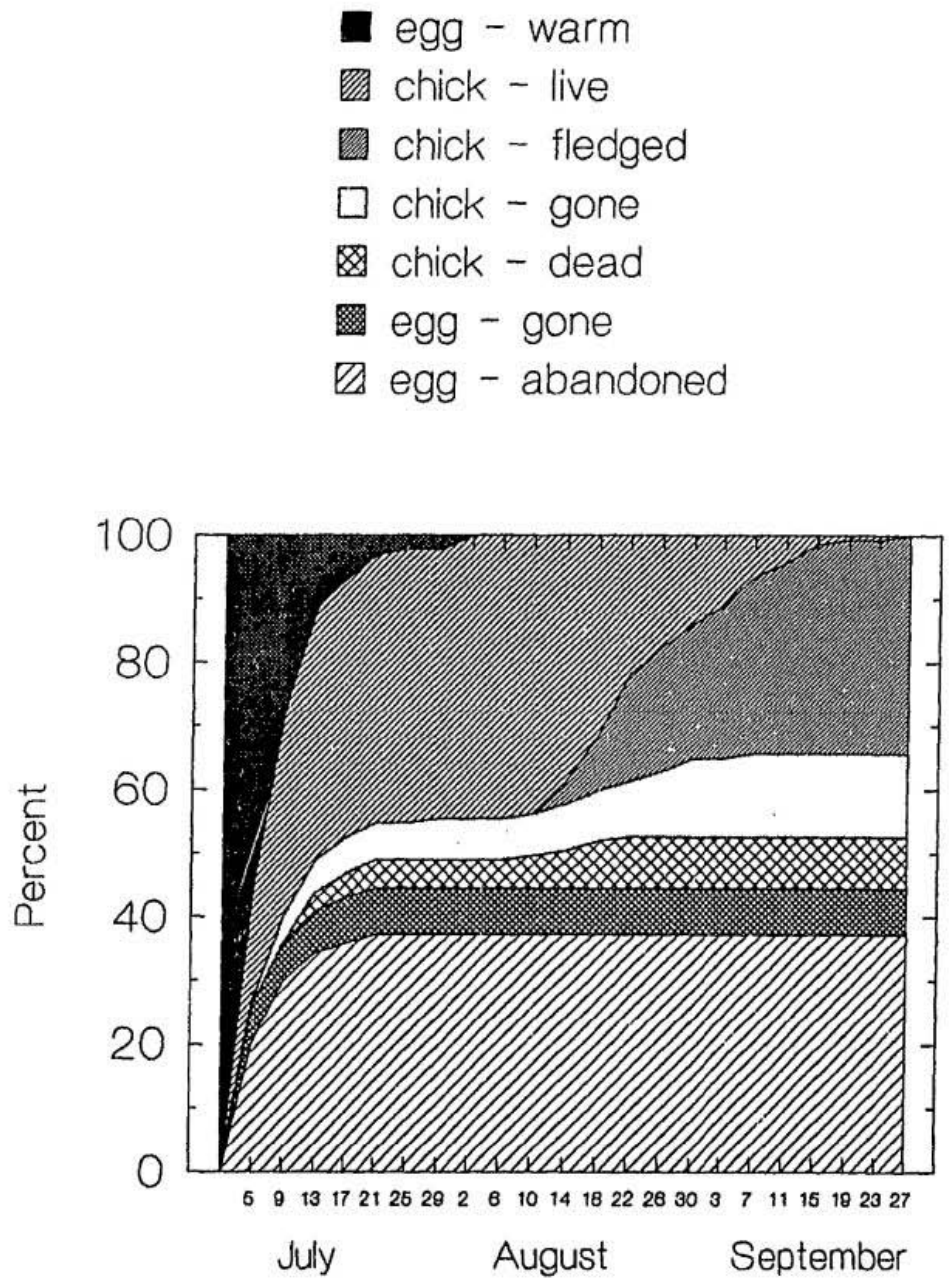


FIGURE 10. Fate of Atlantic Puffin eggs on Great Island in 1992.

of their burrow, especially on level ground, would often dive back down their burrow rather than attempt to fly away. Records were kept of the presence of adults in burrows during burrow inspections to determine how frequently they flushed when disturbed. Adults were encountered in 85% of 382 burrow inspections in which there was a warm egg in the nest. Adults were likely present in many of the remaining 15% because I did not explore burrows further once a warm egg was found. There was no significant difference in the frequency that adults were encountered with warm eggs in maritime level (93%), inland slope (85%), and maritime slope (78%) habitats (X^2_2 = 0.86, P = 0.651).

3.3.3. Hatching

Hatching success (per egg laid) was measured only in 1992 and averaged 56% (Table 6). A significant component chi-square allowed me to reject the null-logit model (Table 10). The best model explaining observed hatching frequencies included main effects of location, though this model did not fit the data well (G^2_6 = 10.70, P = 0.098). Success was much higher on the east (z = 3.15, P = 0.002) than on the north (z = -1.31, P = 0.190) and south (z = -1.84, P = 0.066) sides of the island (Table 6). Although differences by habitat were not significant (Table 10), proportions of eggs hatched were consistently lower in level habitat than in maritime slope habitat (Fig. 9). The trend across habitats differed by location with inland plots having highest success in the east and south and lowest success in the north (Fig. 9).

TABLE 10. Summary of logit-model analysis of the frequency of Atlantic Puffin chicks hatched per egg laid and per burrow on Great Island in 1992. Terms were added hierarchically in the order listed.

	Per egg laid			Per burrow		
Source	G^2	df	P	G^2	df	P
Null-logit	22.72	8	0.004	23.43	8	0.003
Due to L[a]	12.02	2	0.003	11.79	2	0.003
Due to H	2.43	2	0.297	1.37	2	0.503
Due to L*H	8.27	4	0.082	10.27	4	0.036

[a] L = location; H = habitat.

The component chi-square for the interaction effect of location by habitat was significant when proportions of chicks hatched per burrow were considered (Table 10). Thus, the best model in this case was the saturated model. Partial components supported a main effect by location but not by habitat. The modifying effects of habitat on the trends by location were most apparent at inland plots. Significant interaction effects were found at the inland plots on the north ($z = -3.11$, $P = 0.002$) and east ($z = 2.32$, $P = 0.021$) sides of the island and in the level plot at the north end ($z = 1.99$, $P = 0.047$).

Proportion of variance within plots was 85% for hatching success and 88% for chicks hatched per burrow. There was no significant relationship between burrow density and mean hatching success ($r^2 = 0.12$, $F_{1,7} = 0.96$, $P = 0.360$) or mean number of chicks hatched per burrow ($r^2 = 0.04$, $F_{1,7} = 0.32$, $P = 0.592$). Distance from edge, slope and aspect also had no significant effect on mean hatching success ($r^2 = 0.52$, $F_{3,5} = 1.79$, $P = 0.266$) and mean number of chicks hatched per burrow ($r^2 = 0.29$, $F_{3,5} = 0.68$, $P = 0.599$). Aspect made the most substantial contributions to sample variance in mean hatching success (part $r^2 = 0.44$, $F_{1,5} = 4.59$, $P = 0.087$) and mean number of chicks hatched per burrow (part $r^2 = 0.24$, $F_{1,5} = 1.70$, $P = 0.249$), with success higher at east than west aspects.

Hatching success was related to nest flooding. Eggs hatched in 67% ($N = 89$) of dry burrows and 33% ($N = 48$) of wet burrows ($X^2_1 = 14.66$, $P = 0.0001$; Table 11). Proportions of eggs that hatched from nests that flooded in heavy rains differed

TABLE 11. Numbers of Atlantic Puffin eggs that hatched in wet and dry burrows in study plots on Great Island in 1992.

			Wet		Dry	
Plot	Location[a]	Habitat[a]	Hatch	Not hatch	Hatch	Not hatch
2E-120	N	MS	0	1	8	3
2E-85	N	ML	2	5	6	3
5E-70	N	IS	0	6	3	3
5E-280	E	MS	7	1	4	3
5E-230	E	ML	1	2	8	4
7E-220	E	IS	3	1	13	1
10E-5	S	MS	2	7	5	2
9W-20	S	ML	0	8	5	4
9E-95	S	IS	1	1	8	6
Total			16	32	60	29

[a] N = north, E = east, S = south; MS = maritime slope, ML = maritime level, IS = inland slope.

among locations and habitats. Eggs hatched in 73% (N = 48) of wet burrows at east location compared to 14% (N = 40) at north and 16% (N = 49) at south locations (X^2_2 = 15.72, P = 0.0004; Table 11). Hatching success in wet burrows was higher in maritime slope (50%, N = 43) than in maritime level (17%, N = 48) habitat (X^2_1 = 4.50, P = 0.034) and was intermediate in inland slope habitat (33%, N = 46). There were no significant differences in hatching success in dry burrows across locations (X^2_2 = 1.85, P = 0.398; Table 11) or habitats (X^2_2 = 0.39, P = 0.824).

Seventeen percent (N = 76) of eggs that later hatched were cold on at least one check; one late-hatching egg was cold on six checks. Hatching success was highest on the east side at plots in maritime slope (73%, N = 15) and inland slope (89%, N = 18) habitats, both of which retained water for short periods of time compared to plots in the same habitats on the north and south sides. None of the eggs that were floating in burrows at southern plots subsequently hatched.

3.3.4. Chick mortality

Many chicks that failed to fledge were found dead in burrows in 1992 (38%, N = 47; Fig. 10) and 1993 (80%, N = 40). Early hatching chicks (1-8 July) had higher survival than late hatching chicks (after 8 July) in both 1992 and 1993 (X^2_2 = 10.89, P = 0.004; Fig. 11) even though capelin were not seen in puffin food loads until 8 July in 1992 and 6 July in 1993 (Rodway unpubl.). Disturbance may have confounded this relationship but chick survival was not related to the number of

times incubating adults were disturbed before hatching (X^2_2 = 0.41, P = 0.815). Much (67%) of the early mortality was associated with nest flooding. The proportion of chicks that died in the first two weeks of July 1992 was higher in wet burrows (6 of 8) than in dry burrows (3 of 58; X^2_1 = 30.62, P < 0.0001).

I observed Herring Gulls eating two dead, muddy puffin chicks from my study plot during all-day watches in 1993. I saw no live chicks taken from study burrows, but incidental observations of Herring and Great Black-backed Gulls killing near-fledging and fledging puffin chicks were frequent. Gulls caught chicks that approached the entrance of their burrow during the day or as they were fledging in the night. Most depredated chicks found in 1992 were probably caught while fledging (77% of carcasses had wing lengths $\geq$ 140 mm, N = 47; see Nettleship 1972, Harris 1984, Rodway unpubl.). More depredated fledglings found in the vicinity of main study plots in 1992 (N = 34) were on inland slope (68%) than on level (26%) and maritime slope (6%) habitat.

3.3.5. Fledging success

Fledging success (per chick hatched) was measured only in 1992. Success was highest in plots at south locations and was generally higher in maritime slope plots (Table 6; Fig. 9). Differences due to location or habitat were not significant when the full contingency table was analyzed (Null-logit: G^2_8 = 11.49, P = 0.176), although z-tests of lambdas showed a significant effect for plots at the south end

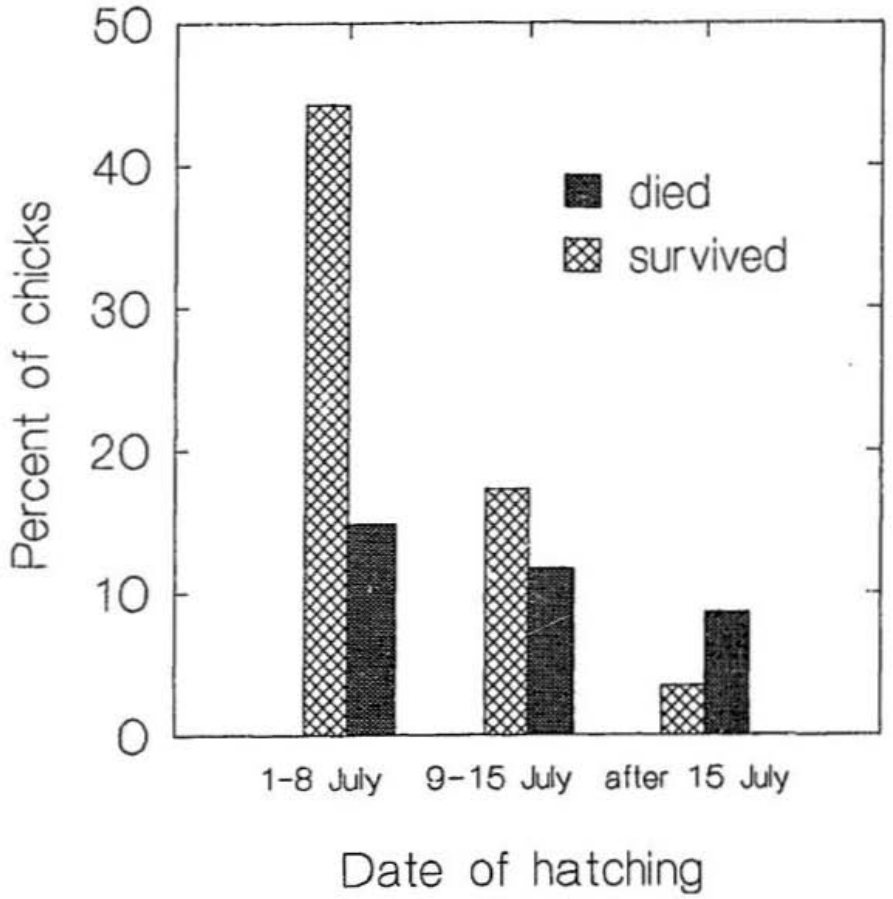


FIGURE 11. Survival of Atlantic Puffin chicks in relation to hatching date on Great Island in 1992.

($z = 2.36$, $P = 0.019$). Analyses of tables that were collapsed to increase expected cell frequencies gave similar results (Location: $G^2_2 = 4.94$, $P = 0.084$; Habitat: $G^2_2 = 2.21$, $P = 0.332$) and likelihood ratio and Pearsonian chi-squares lead to the same conclusions.

Within plot variance for fledging success was 87%. There was no significant relationship between mean fledging success per plot and burrow density ($r^2 = 0.19$, $F_{1,7} = 1.65$, $P = 0.240$) or distance from edge, slope and aspect ($r^2 = 0.71$, $F_{3,5} = 3.99$, $P = 0.085$) when all plots were considered. Fledging success at plot 5E-70, discussed earlier, had a large influence on the results of analyses. Only three eggs hatched and two chicks fledged at that plot, giving a relatively high estimate for mean fledging success. Density accounted for 33% of the variation in mean fledging success ($F_{1,6} = 2.97$, $P = 0.136$) and the model including distance from edge, slope, and aspect accounted for 86% if plot 5E-70 was excluded (Table 12). Distance from edge explained most of the variance; slope and aspect contributed little.

3.3.6. Breeding success

Breeding success (chicks fledged per egg laid) averaged 34% in study plots in 1992 (Table 6). Assuming similar numbers of eggs laid in control plots as in study plots provides an estimate of 55% for breeding success in control plots. Success was higher in 1993 ($X^2_1 = 34.58$, $P < 0.0001$), averaging 68% (Table 7). I was unable to reject the null-logit model for the contingency table of breeding success by

TABLE 12. ANOVA summary for multiple regressions of mean number of Atlantic Puffin chicks fledged per chick hatched in 1992, and per egg laid in 1992 and 1993 on Great Island on distance from the shore edge of the colony, slope, and aspect. Year was included as a dummy variable to control for differences between years. Variables were added hierarchically in the order listed.

Source	r^2	Standard coefficient	Mean square	df	F	P
Mean number of chicks fledged per chick hatched[a]						
Distance	0.78	-0.884	0.247	1	22.45	0.009
Slope	0.05	-0.227	0.014	1	1.27	0.323
Aspect[b]	0.03	0.312	0.009	1	0.82	0.416
Full model	0.86		0.090	3	7.88	0.037
Residual			0.011	4		
Mean number of chicks fledged per egg laid						
Year	0.40		0.426	1	16.38	0.001
Distance	0.12	-0.449	0.128	1	7.26	0.016
Slope	0.11	0.433	0.120	1	6.82	0.019
Aspect	0.01	0.068	0.005	1	0.19	0.676
Full model	0.64		0.170	4	6.53	0.003
Residual			0.026	15		

[a] Excluding plot 5E-70; see text.

[b] Aspect coded from southeast = 0 to northwest = 180; see Methods.

location by habitat in 1992 (G^2_8 = 7.51, P = 0.483), even though success in maritime slope habitat was 76% higher than in maritime level habitat (Table 6, Fig. 9). The null-logit model was also the most parsimonious model fit to the data in 1993 (contingency tables were collapsed to maintain adequate cell frequencies: fledge by location: G^2_2 = 0.70, P = 0.704; fledge by habitat: G^2_2 = 2.36, P = 0.307).

Data from 1992 and 1993 were combined to increase sample size for tests of regression models relating mean breeding success to burrow density and distance from edge, slope, and aspect. Year was included as a dummy variable to control for differences between years. Within plot variance was 81%. Burrow density was not significantly related to mean breeding success (part r^2 = 0.05, $F_{1,17}$ = 1.69, P = 0.211) after differences between years were considered. Distance from edge and slope but not aspect added significantly to explained variance after effect of year was accounted for (Table 12).

3.3.7. Chicks fledged per burrow

The proportion of burrows that fledged chicks in growth study plots averaged 26% compared to an average of 42% in control plots in 1992 (Table 6). Differences between control and study plots were similar across habitats ($F_{2,4}$ = 0.10, P = 0.908) and locations ($F_{2,4}$ = 2.17, P = 0.230), although differences tended to be lower on the east than on the north and south sides (Table 6, Fig. 12). Logit-model analysis

was carried out on the four-dimensional contingency table of fledge by type of plot by location by habitat. The composite component chi-square for the null-logit model was significant at the 0.005 level (Table 13). Partial components for third- and second-order interactions were not significant, but all first order interactions made significant contributions to the fit of the model. Thus, the final model included main effects of type of plot, location and habitat (G^2_{12} = 10.16, P = 0.602). Z-tests for lambdas showed significant, positive deviations for south location and for maritime slope habitat, and significant decrements from average for north location and for maritime level habitat (Tables 6 and 14).

Chicks fledged per burrow was higher in 1993 than in 1992 (X^2_1 = 26.96, P < 0.0001; Table 7). Success in 1992 study plots was almost twice as high in 1993 as in 1992 (X^2_1 = 12.81, P = 0.0003). Numbers of chicks fledged from burrows in 1992 control plots was also higher in 1993 (X^2_1 = 6.47, P = 0.011) and was similar to that in new plots (X^2_1 = 0.75, P = 0.387). Analysis of the four-dimensional logit-model for the frequency of chicks fledged per burrow in 1993 yielded significant main effects due to type of plot, location and habitat (Table 13). There was no evidence of effects due to interactions; the model including main effects fit the data well (G^2_{12} = 13.62, P = 0.326). Differences in 1993 between 1992 study and control plots suggest a residual effect of the disturbance to study plots in 1992, as study and control plots from 1992 received the same treatment in 1993. Results were similar to those observed in 1992: the highest proportion of chicks fledged per

TABLE 13. Summary of logit-model analysis of the frequency of Atlantic Puffin chicks fledged per burrow on Great Island in 1992 and 1993. Terms were added hierarchically in the order listed.

	1992			1993		
Source	G^2	df	P	G^2	df	P
Null-logit	35.70	17	0.005	44.35	17	0.000
Due to T[a]	9.79	1	0.002	4.43	1	0.035
Due to L	7.87	2	0.020	6.24	2	0.044
Due to H	7.88	2	0.020	20.48	2	0.000
Due to T*L	2.36	2	0.307	0.53	2	0.767
Due to T*H	0.42	2	0.811	1.70	2	0.427
Due to L*H	5.21	4	0.266	7.39	4	0.117
Due to T*L*H	2.10	4	0.717	4.00	4	0.406

[a] T = Type of plot; L = location; H = habitat.

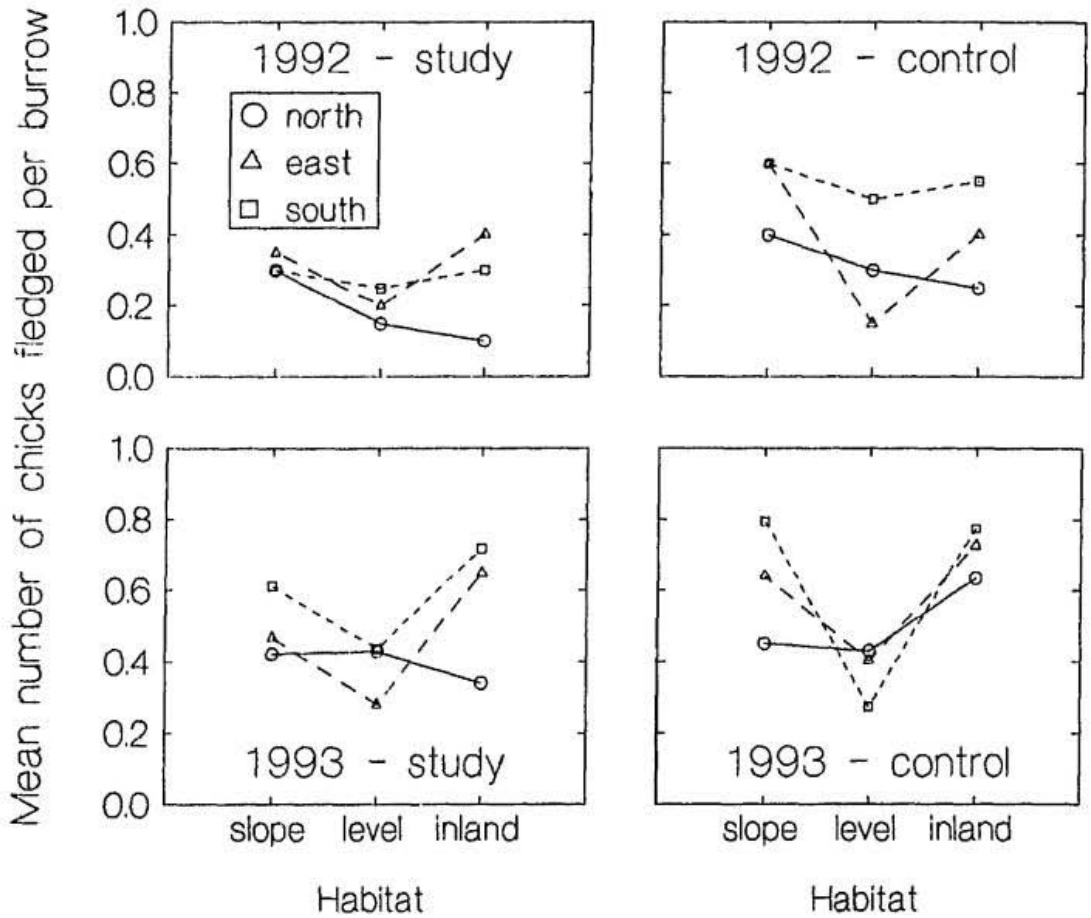


FIGURE 12. Interaction of habitat and location for mean number of Atlantic Puffin chicks fledged per burrow on Great Island in 1992 and 1993.

TABLE 14. Lambda estimates and z-tests on lambdas for effects of Type of plot, Location and Habitat on the frequency of Atlantic Puffin chicks fledged per burrow on Great Island in 1992 and 1993.

	Type of plot		Location			Habitat		
	Study	Control	North	East	South	Slope	Level	Inland
1992								
Lambda	-0.169	0.169	-0.204	0.026	0.178	0.199	-0.180	-0.019
z	-2.899	2.899	-2.385	0.318	2.067	2.513	-2.130	-0.383
P	0.004	0.004	0.017	0.750	0.039	0.012	0.033	0.702
1993								
Lambda	-0.115	0.115	-0.168	-0.001	0.169	0.077	-0.311	0.234
z	-2.104	2.104	-2.215	-0.018	2.233	0.996	-4.115	3.128
P	0.018	0.018	0.013	0.493	0.013	0.160	0.000	0.001

burrow occurred at south location and in inland slope and maritime slope habitats (Tables 7, 14, Fig. 12).

Data from 1992 and 1993 were combined to test regression models for numbers of chicks fledged per burrow. Proportion of variance within plots was 87%. Mean number of chicks fledged per burrow was related to burrow density (part $r^2 = 0.09$, $F_{1,42} = 6.19$, $P = 0.017$) after year and type of plot were considered. Distance from edge, slope, and aspect were significant predictors of fledge per burrow after adjustments were made for differences due to year and type of plot (Table 15).

Plots of response against explanatory variables revealed that the relationship between mean numbers of chicks fledged per burrow and distance from edge was described better by an log function than a linear function (Fig. 4). The plot against slope showed that fledge per burrow peaked at slopes between 20 and 30 ° and the relationship was best fitted with a piecewise linear regression line (Wilkinson 1990). Using the log of distance and a piecewise term for slope significantly increased explained variance from 58 to 66% ($F_{1,38} = 8.70$, $P = 0.005$). The contribution of aspect was not significant when non-linear terms for distance and slope were considered (Table 15). Plots of burrow density against distance from edge, slope, and aspect took similar forms as those for fledge per burrow (Fig. 4).

I analyzed the relationship between mean number of chicks fledged per burrow and burrow density within each habitat to address the assumption of habitat

TABLE 15. ANOVA summary for multiple regressions of mean number of Atlantic Puffin chicks fledged per burrow in 1992 and 1993 on Great Island on distance from the shore edge of the colony, slope, and aspect. Year and type of plot were included as dummy variables to control for differences between years and between study and control plots. Variables were added hierarchically in the order listed.

Source	r^2	Standard coefficient	Mean square	df	F	P
Predicted linear model						
Year	0.24		0.402	1	22.33	0.000
Type of plot	0.08		0.066	2	3.64	0.035
Distance	0.10	-0.309	0.157	1	8.72	0.005
Slope	0.11	0.353	0.189	1	10.50	0.002
Aspect[a]	0.05	0.229	0.072	1	4.08	0.050
Full model	0.58		0.158	6	9.02	0.000
Residual			0.018	40		
Non-linear model						
Year	0.24		0.402	1	27.16	0.000
Type of plot	0.08		0.066	2	4.43	0.019
Log distance	0.16		0.264	1	17.80	0.000
Piecewise slope[b]	0.17		0.095	3	6.42	0.001
Aspect	0.01		0.008	1	0.54	0.467
Full model	0.66		0.136	8	9.19	0.000
Residual			0.015	38		

[a] Aspect coded from southeast = 0 to northwest = 180; see Methods.

[b] Breakpoint for piecewise regression was at 25 °.

selection models that fitness or productivity decreases with increasing density. Number fledged increased significantly with density within inland slope habitat (r^2 = 0.27, $F_{1,13}$ = 4.71, P = 0.049) and nonsignificantly within maritime slope (r^2 = 0.05, $F_{1,15}$ = 0.84, P = 0.373) and level (r^2 = 0.05, $F_{1,13}$ = 0.63, P = 0.442) habitats (Fig. 13). Relationships were equally well described, in terms of variance explained, by linear and logarithmic functions.

3.3.8. Relationships between success per burrow in 1992 and 1993

Frequency of chicks fledged in 1993 was higher from burrows that fledged chicks in 1992 than from those that did not for all burrows (78 vs. 39%; X^2_1 = 48.65, P < 0.0001) and for burrows known to have contained eggs in 1992 (81 vs. 38%; X^2_1 = 22.97, P < 0.0001). Proportions of burrows where chicks fledged in 1992 that were successful in 1993 were similar at north (80%), east (74%), and south (80%) locations (X^2_2 = 0.61, P = 0.736). Burrows in maritime level habitat that were successful in 1992 were less likely to be successful in 1993 (65%) than those in maritime (88%) and inland (78%) slope habitats, although differences were not significant (X^2_2 = 5.37, P = 0.068). Differences were significant if only control plots were considered (53 vs. 88 and 81%, respectively; X^2_2 = 7.91, P = 0.019). Burrows that did not fledge chicks in 1992 were more likely to fledge chicks in 1993 in inland slope (53%) than in maritime slope (33%) and level (31%) habitats (X^2_2 = 9.18, P = 0.010), and were less likely to fledge chicks in 1993 at

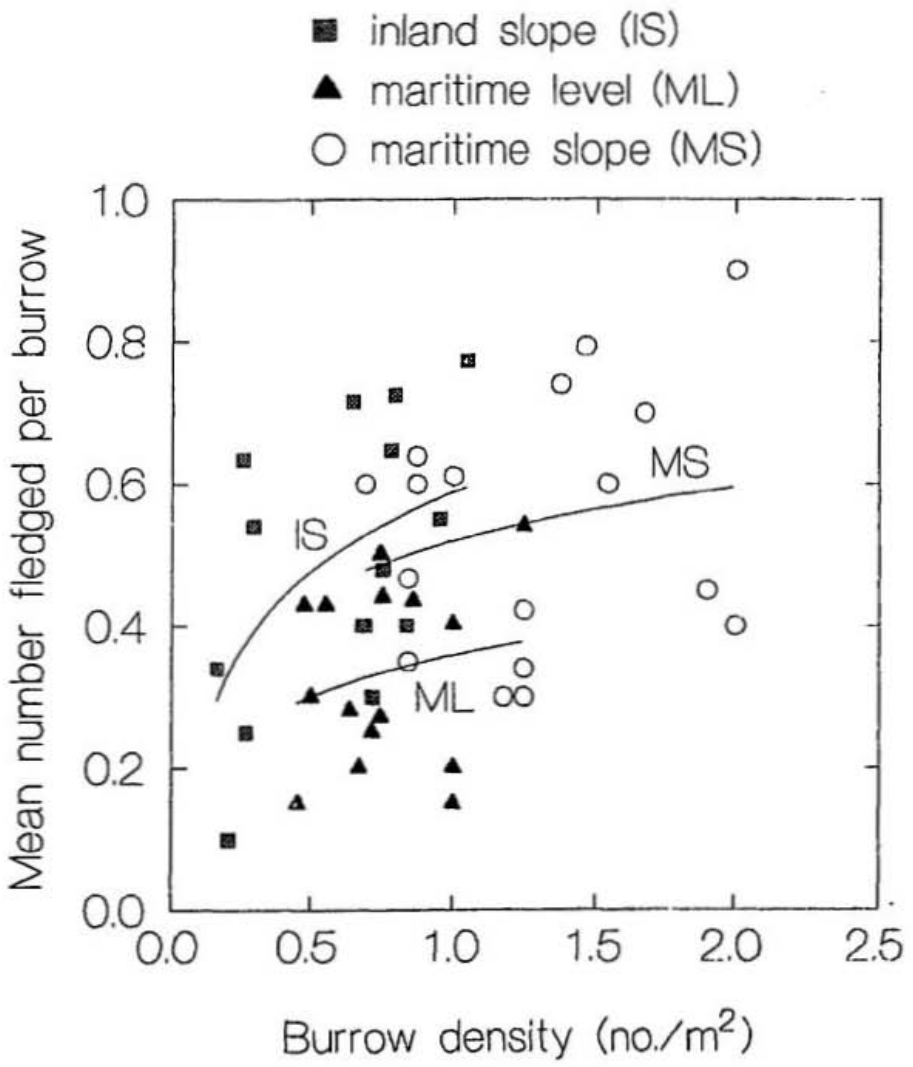


FIGURE 13. Relationships between mean number of Atlantic Puffin chicks fledged per burrow and burrow density in different habitats on Great Island in 1992 and 1993.

north (31%) than at east (42%) and south (46%) locations, but differences by location were not significant (X^2_2 = 4.04, P = 0.133). Burrows that never contained eggs in 1992 fledged chicks in 1993 more frequently from inland slope (57%) than from maritime slope (24%) and level (8%) habitats (X^2_2 = 7.90, P = 0.019), and from south (64%) than from north (20%) and east (17%) locations (X^2_2 = 7.86, P = 0.020).

Chapter 4

DISCUSSION

4.1. Effects of disturbance

The visiting regime used to check burrows in study plots in 1992 reduced breeding success and delayed fledging. Hatching did not appear to be delayed by disturbance (see Sealy 1984) as hatching dates were similar in undisturbed plots in 1993 and overall timing was similar in the two years. Differences between 1992 study and control plots persisted in 1993, suggesting residual effects at least one season following disturbances. Number and timing of visits in 1992 were similar to those used by Nettleship (1972) and Ashcroft (1979) and shown by Ashcroft to cause no reduction in numbers of chicks fledged per burrow as compared to undisturbed controls. Marked reduction in breeding success attributed to the conservative visiting regime used in this study has not previously been reported, although success reported by Nettleship (1972) was similar to that found in study plots in 1992 (Table 16).

Puffins frequently desert their nests following disturbance during the egg-laying or incubation period (Lockley 1934, Kartashev and Myrberget cited in Ashcroft 1979, Korneyeva cited in Nettleship 1972, Harris 1984). Disturbance to incubating or brooding adults near hatching time sometimes causes desertion (Harris 1984) but chick survival after hatch is generally high and is not reduced by subsequent disturbance (Ashcroft 1979, Harris 1984, see also Bertram 1988). Egg desertion

TABLE 16. Summary of breeding performance of Atlantic Puffins on Great Island, Newfoundland in 1968 and 1969 (data from Nettleship 1972) and in 1992 and 1993 (this study and Rodway unpubl.). Data from all habitats and locations were pooled to calculate overall means.

	Nettleship's plots in 1968	Nettleship's plots in 1969	Growth study plots in 1992	Control plots in 1992	All plots in 1993
Eggs laid per burrow (N)	-	-	0.76 (180)	-	0.87 (195)
Eggs hatched per burrow (N)	-	-	0.42 (180)	-	-
Chicks fledged per burrow (N)	-	-	0.26 (180)	0.42 (180)	0.55 (564)
Hatching success (N)	0.57 (150)	0.65 (402)	0.56 (137)	-	-
Fledging success (N)	0.36 (86)	0.57 (261)	0.62 (76)	-	-
Breeding success (N)	0.21 (150)	0.37 (402)	0.34 (137)	0.55[a]	0.68 (169)
Fledging mass [g(N)] [b]	259 (31)	258 (148)	287 (21)	288 (48)	297 (25)
Age at fledging [days(N)]	59 (31)	52 (149)	52 (47)	-	46 (32)

[a] Estimated by assuming similar numbers of eggs laid in control and growth study plots.

[b] Measured within two days of fledging.

following visits early in the breeding cycle is the main reason reported for reduced breeding success caused by observer disturbance in other burrow or crevice-nesting alcid species (Thoresen 1964, Manuwal 1974b, Leschner 1976, Sealy 1976, Summers and Drent 1979, Cairns 1980, Pierce and Simons 1986, Wilson and Manuwal 1986, Watanuki 1987, Bertram 1988, Gaston et al. 1988, Piatt et al. 1990, Gotmark 1992). Disturbance resulted in retarded chick development, probably due to delayed hatching, of Tufted Puffin (*Fratercula cirrhata*) chicks in Alaska (Pierce and Simons 1986).

Results of different studies suggest that puffin's reactions to disturbance may vary at different colonies (Evans and Nettleship 1985). Hatching and breeding success averaged 75 and 65% on Hornoy (Barrett et al. 1987), following a visiting regime similar to that used on Great Island. Ashcroft's (1979) visiting regime on Skomer Island was the same as that used in this study except that she also included visits at the beginning of the season to determine egg-laying. Laying did not appear to be affected by early inspections and hatching and breeding success averaged 77 and 73%, respectively. Similar disturbance on the Isle of May lowered hatching success to 59% and breeding success to 55%, compared to 74% in burrows disturbed only once during incubation and then not again until after chicks had hatched (Harris 1984). Hatching and fledging success on Great Island in 1969 (Nettleship 1972) were similar to that observed in 1992 using similar inspection regimes. Reasons for observed differences between colonies are unknown but may

relate to threats of predation, food supply, or habituation to disturbance. Birds already stressed by food shortage may be more likely to abandon breeding efforts when disturbed. Effects of disturbance may bias inter-colony comparisons especially if visiting regimes differ (e.g., Nettleship 1972).

Effect of disturbance on breeding success was similar across habitats, and thus was independent of burrow density and any differences in age, experience or fitness of breeders that may be associated with position in the colony at a particular location (Coulson 1968, 1988, Coulson and Thomas 1985).

Comparing results from different types of plots in 1992 and 1993 provides some insight into possible timing and causes of increased failure in disturbed plots. Similar numbers of chicks fledged per burrow in 1993 from 1992-control plots and new plots established in 1993 suggested that a single check for eggs during the incubation period did not increase desertion. Measures of breeding success derived from inspecting burrows once during incubation and not again until after chicks have hatched are typically high (73 to 93%) during years of adequate food supply (Harris 1984, Barrett et al. 1987, Harris and Bailey 1992). In 1992, 36 (26%) eggs were deserted or had disappeared when I made the first check for hatching chicks, which followed a single check for eggs during the incubation period. Hatching success would have been typical (74%) if remaining, attended eggs had hatched. I suspect that visits near hatching were responsible for additional egg desertion and may have contributed to delayed chick growth.

Certain recommendations for future studies of puffins on Great Island follow from the observed effects of disturbance in this study. Determining proportions of burrows in which eggs are laid provides estimates for numbers of pairs initiating breeding efforts and is a valuable statistic for comparative analyses of breeding performance and for population monitoring. Numbers of eggs laid can be measured by a single check of burrows in the latter half of the incubation period. A single check will miss a proportion of eggs lost before inspection and some replacement clutches, which will bias success rates upwards, but should provide data comparable among years and locations. Estimates of breeding success can be obtained by subsequent visits after chicks have hatched. Timing of breeding can be roughly back-dated from fledging dates or more accurately from hatching dates determined by observations of first feedings as used in 1993.

4.2. Timing of breeding

Estimated median egg-laying dates in 1992 and 1993 were about one week later than those estimated by Nettleship (1972) in 1968 and 1969. Delayed phenology may have been associated with oceanographic conditions (Birkhead and Harris 1985, Astheimer 1986, Ainley and Boekelheide 1990, Murphy et al. 1991). Sea-surface temperatures were lower and timing of capelin spawning in the vicinity of Great Island was over one month later in 1992 and 1993 than in 1969 and 1970 (Maunder 1971, J. Carscadden, DFO, St. John's, pers. comm.). Puffins may have

responded to environmental or physiological cues (Perrins 1970, Winkler and Walters 1983, Toft et al. 1984, Martin 1987, Monaghan et al. 1992, Bolton et al. 1993) or have been constrained by insufficient female nutrient reserves required to produce eggs (Lack 1968, Drent and Daan 1980, Winkler 1985, Arcese and Smith 1988, Safina et al. 1988). Changes in food availability were probably responsible for delayed laying and extremely low productivity by Black-legged Kittiwakes (*Rissa tridactyla*) (Regehr 1994) and Herring Gulls (Rodway unpubl.) on Great Island in 1992 and 1993 compared to previous years (Maunder and Threlfall 1972, Pierotti 1982). More eggs were laid and overall productivity was higher in 1993 than 1992 for puffins and kittiwakes, suggesting that food shortage was less severe in 1993 than 1992. If birds were constrained by inadequate nutrient reserves, I would have expected egg-laying to be earlier in 1993 than 1992. Similar phenology in the two years for both species suggests that egg-laying was timed by other proximate cues.

Hatching was earlier at south than north and east locations in 1992. This was expected if south is a preferred location and puffins are distributed according to competitive abilities (see below). An alternative explanation is that timing was constrained by burrow and soil conditions in the spring (Hornung and Harris 1976, Harris 1984). Many burrows on north-facing slopes were blocked with ice on 9 May 1992 and burrow temperatures were higher at south than north and east locations in early June 1993. Median hatching dates in 1968 and 1969 were only three days earlier than the median at south location in 1992. Egg-laying was estimated to begin

on 9 May in 1968 and 1969 (Nettleship 1972) and on 19 May in 1992 and 1993. Greater difference between first than median lay dates suggests that laying was more synchronous, at least for the first half of the egg-laying period, in 1992 and 1993 than in 1968 and 1969. Comparing proportions of eggs laid 4 to 7 and 8 to 11 days before median dates in the two study periods supports this idea ($X^2_1 = 8.84$, $P = 0.003$; data calculated from Fig. 8 in Nettleship 1972). Birds prevented from laying early by frozen burrows could result in such a compression of lay dates.

Aspect was the most important predictor of hatching and fledging dates, supporting the idea that spring soil conditions influenced phenology. Earlier timing at south locations and west aspects suggests that prevailing warm winds as well as insolation helped thaw and warm burrows. Factors that affected timing were different than those that affected productivity. Timing was not related to burrow density or distance from edge, and was negatively related to slope, while productivity measures were related to density, distance from edge, and, positively, to slope. This suggests that timing was governed by environmental conditions unrelated to foraging or other abilities of individual birds. Puffins have a protracted breeding season and are often the earliest species to lay within a colony (Harris 1984, Birkhead and Harris 1985). Geographic and latitudinal differences as well as within colony differences in phenology are generally associated with spring temperatures and timing of spring thaw for puffins (Belopol'skii 1957, Harris 1984, Harris and Birkhead 1985) and other boreal or arctic species (Sealy 1975, Kilpi 1992, Williams and Rodwell 1992),

although effects of nest accessibility and prey availability may be confounded (Birkhead and Harris 1985).

Greater differences between locations in fledging than in hatching dates offers support for an ideal despotic distribution and for the prediction that the stress of provisioning chicks will accentuate differences between higher and lower quality birds, but differences appeared primarily due to levels of disturbance in study plots. Differences across locations for fledging dates in control plots were similar to differences in hatching dates in study plots.

Hatching and fledging dates did not differ across habitats. This is similar to Nettleship's (1972) findings for maritime slope and level habitats. Contrary to what Nettleship found, hatching synchrony was greater on level than on slope habitat, though burrow density was lower on level than slope habitat. This contrasts with greater synchrony at higher densities noted for murres (Birkhead 1977) and larid species (Patterson 1965, Gochfeld 1980). Puffins on level habitat are more vulnerable to predation and kleptoparasitism (Nettleship 1972) and protection or swamping tactics such as increased synchrony (Lack 1968, Wittenberger and Hunt 1985) may have higher benefits there than on slope habitat. Perhaps puffins have adjusted their timing on level habitat during a period of increasing gull populations (Nettleship 1972, Pierotti 1982, Cairns et al. 1989) since Nettleship's study. Harris (1980) found no difference in synchrony for puffins nesting at high and low densities with different predation risks, but nests were very sparse in his low density areas and

increased synchrony probably conferred little benefit. Social facilitation to increase synchrony may also have been lacking in such sparse groups (Darling 1938, Gochfeld 1980).

4.3. Breeding success

4.3.1. Egg-laying

Proportions of burrows with eggs were high and were similar to those reported at British colonies during periods of normal productivity (Ashcroft 1979, Harris 1980, 1984). Numbers found in this study may under-estimate total eggs laid because some eggs may have been lost before burrows were checked. Estimates on Great Island also may be biased downward compared to those of Harris (1980) because I included all burrows and Harris included only those with signs of occupation. I found that signs such as fresh digging or droppings at the entrance to burrows were not good indicators of occupancy. Entrances to many burrows that contained eggs and fledged chicks were obscured by grass and showed no obvious signs of habitation throughout the season, while others that never contained eggs looked persistently occupied.

Lower proportions of burrows with eggs suggests that fewer birds initiated breeding efforts in 1992 than in 1993. This may have been a response to food supply as productivity of puffins, kittiwakes, and *Larus* gulls was lower in 1992 than 1993. Ashcroft (1979) noted similar variation in three years on Skomer Island and

thought that reduced egg-laying was associated with poor spring feeding conditions. However, lower numbers of eggs corresponded with much later laying in her study, which I did not observe on Great Island. Inter-year variation of the magnitude recorded in this study is common in surface-feeding species such as kittiwakes and is probably related to climatic and oceanographic conditions and food availability (Hatch and Hatch 1990, Murphy et al. 1991, Neuman 1994, Regehr 1994). For diving species like puffins, proportions of pairs laying eggs are typically high (Gaston and Nettleship 1981, Harris 1980) and less responsive to fluctuations in prey availability (Hatch and Hatch 1990).

Proportions of burrows containing eggs showed no consistent trends by habitat or location. Proportions did increase with burrow density, and decrease with increasing distance from edge and slope. Harris (1980) also found that greater proportions of burrows contained eggs in dense than sparse nesting areas. The negative effect of slope reflected lower proportions of eggs laid in maritime slope habitat in 1992 and in inland slope habitat in 1993. Lower numbers of eggs laid on steeper slopes was opposite to predictions. Reasons for this trend are unclear, especially considering that chick productivity was positively related to slope, but may include abandonment of burrows on steep maritime slopes because of increasing erosion, and greater proportions of new, unoccupied burrows on inland slopes (see below).

4.3.2. Hatching

Hatching success was most affected by disturbance and environmental conditions. Unseasonably heavy rains caused burrow flooding and resulted in abandonment and failure of some eggs. Higher hatching success observed at east location and in maritime slope habitat was related to the degree and duration of burrow flooding. Puffin eggs can probably withstand temporary periods of flooding and cooling, but not extended periods (see Sealy 1984, Gaston and Powell 1989, Astheimer 1991). Soil drainage varied across sites, but not in a predictable manner in relation to the habitat categories used in this study. This indicates that analyses based on categories used here and by Nettleship (1972) may fail to detect effects of important factors such as drainage patterns. I expected slopes near shore to be well drained but flooding was most severe and persistent at the plot in maritime slope habitat at the south end of the island. Slope, rock substrate, soil type and depth, and burrow architecture probably contributed to drainage patterns (Stokes and Boersma 1991, Thompson and Furness 1991).

Survival of small chicks was also reduced in wet burrows. Mean temperatures in July 1992 and 1993 were 3 °C cooler than 30-year averages (Atmospheric Environment Service, St. John's). Temperatures were most depressed early in July when most chicks were hatching and may have exacerbated effects of flooding. Excessive rainfall and colder temperatures have been associated with poor breeding success in a number of studies, causing direct mortality of eggs and young and

possibly reducing prey availability and foraging efficiency (Nettleship 1972, Vermeer 1978, Konarzewski and Taylor 1989, Baird 1990, Murphy et al. 1991, Stokes and Boersma 1991, Thompson and Furness 1991, Norman et al. 1992, Chastel et al. 1993).

Overall hatching success in 1992 was the same as Nettleship (1972) observed in 1968 under similar weather conditions and disturbance levels (Table 16). That inclement weather reduced success in two out of four years of studies of puffins on Great Island suggests that it may be a common contributor to breeding failure. In study plots at east location, which were well drained, hatching success in 1992 was similar to that recorded in slope habitat in 1969 (Nettleship 1972) and to average values reported for British and Norwegian colonies (Ashcroft 1979, Harris 1980, Barrett et al. 1987). Thus, drainage patterns affect breeding success and should influence habitat quality and the habitat choices birds make. Differences in success between slope and level habitat support this idea but highest hatching success and lowest fledging success at east location suggest that other factors are more important determinants of preferred and optimal habitat than soil drainage.

Most eggs that failed to hatch were abandoned in the nest and removed later by puffins cleaning out their burrows. I suspected that most of the eggs that disappeared had also been abandoned and had been cleaned out before the burrow was checked. Herring Gulls regularly patrolled puffin habitat and were observed eating abandoned eggs that had been cleaned out of burrows, but there was no

indication that they preyed on viable eggs. Chicks that die in the nest are also removed by parents (Lid 1981, Anker-Nilssen 1987; this study).

I found no evidence that puffins flush out of burrows in panic flights or displace eggs towards the entrance of their burrows when disturbed as reported by Nettleship (1972) and Baird (1990). The majority of adults remained in their burrows when disturbed. Harris (1984) noted that after breeding has been initiated, puffins that are standing outside burrows tend to dive back down their burrows when disturbed rather than fly away. This was especially true on level habitat on Great Island and may reflect the relative predation risks of withdrawing to the safety of the burrow or attempting to escape. Puffins gain protection from aerial predators by nesting in burrows and it would seem maladaptive for incubating birds to flush from their eggs every time aggregations of off-duty and nonbreeding birds flush off nesting slopes in response to frequent gull alarm cries. Invasion by a terrestrial predator (e.g., humans) may elicit an escape response and explain observations reported by Nettleship (1972) and Baird (1990), though this was not observed during my investigations. Observations of eggs that are displaced and depredated after they have been abandoned could confuse interpretations. Also, in longer burrows puffins frequently place eggs towards the entrance (Lockley 1934, pers. obs.) which could be misinterpreted as displacement.

Nettleship (1972) attributed habitat differences in hatching success to greater displacement and subsequent predation of eggs in level than slope habitat. Though

not significant in this study, differences in hatching success between maritime level and maritime and inland slope habitats (15%), were similar in magnitude to those between level and slope habitat (19%) observed by Nettleship. If eggs are not displaced from burrows, how do we explain consistent differences between habitats? Desertion is the commonest cause of hatching failure even in the absence of human disturbance (Harris 1984). Given clement weather and abundant food, egg abandonment may result from adult mortality or lack of coordination between mates. On Great Island, Great Black-backed Gulls catch most puffins on the ground and hunt almost exclusively on level or gently sloping habitat where they catch adults at their burrows (pers. obs.). Predation on adults was not sufficient to account for reduced hatching success, but greater adult mortality would change the demography of the nesting population as well as make level habitat less attractive to prospecting birds. The net result would be a higher proportion of young, inexperienced breeders and less competitive individuals on level than on slope habitat. I have no data to evaluate this idea, but the low attendance on and the high frequency of panic flights from level habitat (Nettleship 1972, Evans 1975, pers. obs.) is consistent with a perceived predation threat (Harris 1980). Herring Gulls are not a threat to adult puffins and freely mingle with them, while Great Black-backed Gulls are the only serious predator of adults on Great Island and elsewhere (Lockley 1934, Brooke 1972, Flegg 1972, Evans 1975, Harris 1980, 1984) and are given a wide berth by puffins on the ground (pers. obs.).

4.3.3. Fledging

Fledging success of puffins typically exceeds 90% when food is not scarce (Ashcroft 1979 [note that estimate of 74% in 1974 reported by Ashcroft in Table 6 is probably an error and should read 94% given figures for hatching and breeding success], Harris 1980, 1984, Barrett et al. 1987). Most chick mortality normally occurs during the first 10 days of life (Harris 1984). When food is less available nestling mortality can be extreme and protracted (Lid 1981, Harris 1984, Anker-Nilssen 1987, Barrett et al. 1987, Barrett and Rikardsen 1992).

Fledging success in different habitats and locations on Great Island has ranged from 21 to 81% (Nettleship 1972, Brown and Nettleship 1984, this study). Highest success occurred at south location in 1992 and in maritime slope habitat in 1968, 1969, and 1992. Chick survival did not appear affected by disturbance in 1992 and the most likely cause of mortality in all years was directly or indirectly linked to food supply (Nettleship 1972, Brown and Nettleship 1984, Nettleship 1991, Rodway unpubl.). Most chicks that failed to fledge in 1993 were found dead in their burrows. Fewer were found in 1992, but differences between years were probably due to the fact that I was better able to document the fate of chicks during all-day watches in 1993. Proportions of chicks that died in their burrows were probably higher than results indicated because some dead chicks were cleaned out of burrows by adult puffins or washed out during heavy rains. Starvation appeared to be the primary cause of death (Rodway unpubl.).

Breeding success in 1993, in burrows subjected to minimal disturbance, was similar to that reported by Ashcroft (1979) on Skomer Island, and was in the lower range of values reported by Harris (1980, 1984, Harris and Bailey 1992) on St. Kilda and the Isle of May. If I assume an average hatching success of 75% in 1993, then fledging success was probably close to 90%, and could be considered normal in that year. As noted above, food shortage appeared less severe in 1993 than in 1992 and, judging from numbers of eggs laid and chicks fledged, may not have had a major impact on puffins in 1993 (Table 16). Reduced success in 1992 may reflect more difficult feeding conditions. Inclement weather may have affected prey availability and contributed to low success in 1968 (Nettleship 1972). Success in 1968 was similar to 1981 when capelin were less available (Brown and Nettleship 1984, Nettleship 1991). Food also may have been limiting in 1969 because fledging success in 1969 was lower than in 1992 in both slope and level habitats (Nettleship 1972) and fledging masses were higher in 1992 and 1993 than in 1968 and 1969 (Table 16; Rodway unpubl.).

In 1992, fledging success was primarily related to distance from edge and not to slope. This may have been true in Nettleship's study as well because slope habitat was generally closer to the shore edge of the colony than level habitat. However, both distance from edge and slope were important predictors of breeding success and numbers of chicks fledged per burrow in 1992 and 1993. Higher numbers of chicks

fledged per burrow on maritime and inland slope habitats than on level habitat in 1993 implies an advantage to puffins nesting on slope habitat.

Nettleship (1972) found that puffins nesting further from shore on level ground suffered greater kleptoparasitism by gulls than those nesting close to shore on slope. He hypothesized that high rates of kleptoparasitism reduced chick provisioning on level habitat and resulted in increased predation of chicks that, when hungry, tended to spend more time near burrow entrances where they were accessible to predatory gulls. Data from 1981 are not consistent with this idea. Proportions of prematurely disappearing chicks that may have been taken by gulls was lower, and proportions of chicks found dead in burrows was higher in 1981 when food was less available than in 1968-69 (Brown and Nettleship 1984). I also found that kleptoparasitism increased with distance from the shore (Rodway unpubl.). However, highest rates were on inland slope and not on level habitat. Fledging success was not related to kleptoparasitism at a particular study site, and provisioning rate was positively related to kleptoparasitism because birds delivering the most food to their chicks were also kleptoparasitized most frequently.

Differences in the quality of nesting birds offer an alternative explanation for variation in success across habitats and locations. Starvation was the main cause of chick mortality in 1992 and 1993, and appeared to be due to the inability of parents to provision chicks adequately (Rodway unpubl.). Provisioning skills increase with age and experience in some species (Ryder 1980, Burger 1988, Nelson 1988) and

differences in numbers of chicks fledged by location and habitat may be explained by greater proportions of young, inexperienced, and less capable birds at north and east than at south locations and in level than in slope habitat. Higher correlation between burrow success in 1992 and 1993 in slope than in level habitat adds support to the idea that established, skilled breeders were more common in slope habitat. Also, in burrows that were not used for breeding in 1992, chicks were more likely to fledge in 1993 at south than at north and east locations, and in slope than in level habitats. This suggests that burrows in more successful areas were more attractive or that birds that were recruiting to those areas in 1993 were of higher quality (see Porter and Coulson 1987, Porter 1988, 1990). Greater success for early-hatching than late-hatching chicks may also be a function of the quality of nesting birds (see Introduction).

4.4. Effect of stressful conditions

I hypothesized that stressful conditions would reduce the success of inexperienced breeders or breeders in 'marginal' habitat more than that of experienced breeders or breeders in 'optimal' habitat. I assumed an ideal despotic distribution with higher quality individuals occupying preferred habitats. The study anticipated a reduced supply of prey, especially capelin, that would add a stress to birds attempting to raise chicks. Differences in reproductive performance were expected to be most pronounced during the nestling phase due to the relative

energetic costs of egg-laying and raising young. Observations of prey being delivered by puffins and by other nesting species suggested that capelin was less available to breeding seabirds during the 1992 and 1993 seasons than in more typical years (Maunder and Threlfall 1972, Pierotti and Annett 1987, Nettleship 1991, Regehr 1994, Rodway unpubl.). Thus, conditions were appropriate for testing the predictions made.

Analyses of results from study plots in 1992 gave little evidence to support predictions. Numbers of eggs laid were lower in the north than in the east or south, but differences were not significant. Proportions of burrows with eggs were similar across habitats. Hatching success differed significantly by location and was highest on the east side and similar on the north and south sides. Maritime level habitat had consistently lower hatching success than maritime slope habitat. This trend agreed with predictions, but differences were not significant. Fledging success and breeding success differed as predicted across locations and habitats, but lack of significance in statistical tests again prevented inferences to the population. These results suggest possible Type II errors. The effects of disturbance likely contributed to Type II error by effectively reducing sample sizes.

Comparing eggs laid per burrow in study plots with chicks fledged per burrow in study and control plots provides a reliable interpretation of relative changes in reproductive performance over the season and a means to evaluate predictions. Numbers of chicks fledged per burrow in study and control plots in 1992 and 1993

differed significantly across locations and habitats. Results allow inferences that more chicks were produced per burrow at south and west than at north and east locations and in maritime and inland slope than in maritime level habitats. The proportions of burrows containing eggs were determined on initial visits to study plots and were not biased by disturbance. The lack of differences observed in proportions of eggs laid across locations and habitats may reflect low costs of egg production (Montevecchi and Porter 1980, Birkhead and Harris 1985). Subsequent differences in chick production support predictions that most failure should occur during the nestling phase, and that greater differences in reproductive performance between slope and level habitats and between north and south locations should occur during the nestling period than the incubation period, due to the increased stress of provisioning chicks.

4.5. Burrow density

Habitat selection theory generally predicts higher densities in preferred habitats, and in optimal habitats if distribution follows an ideal despotic model (Fretwell and Lucas 1970). Higher burrow density and productivity at south and west locations and in maritime slope habitat suggest that these are preferred and optimal sites and agrees with an ideal despotic distribution. Higher productivity and lower density in inland slope than maritime level habitat does not fit predictions. Burrow density was primarily related to distance from edge while burrow productivity was

related to distance from edge and slope. This suggests that preferred sites are close to the shore edge of the colony and optimal sites are on slope.

Decreasing density with increasing distance from the shore edge of the colony may reflect patterns of colonization. Puffin populations on Great Island have increased this century (Nettleship and Evans 1985). Changes in vegetation indicate colony expansion has occurred from the shore inland. New burrows are being dug in tall herbaceous vegetation and under live trees towards the interior of the island (pers. obs.). Older, eroded areas have been and are being abandoned. Numbers of burrows in Nettleship's main study area decreased 25% between 1969 and 1979 (Cairns and Verspoor 1980). Puffins are known to colonize, erode and abandon nesting areas over periods of 50-100 years (Harris 1984).

Higher burrow density on slope than level ground is typical of alcid colonies (Richardson 1961, Nettleship 1972, Evans 1975, Wilson and Manuwal 1986, Gaston 1992). It is probably a function of preference, because alcids have high wing loading and find it difficult to become airborne from level ground, and physical limitations imposed by the volume of soil available for burrowing at different slopes (Harris 1984, Harris and Birkhead 1985). Burrow density peaked at slopes of 20 to 30 ° on Great Island. It is possible that the colony is shifting from the steepest slopes because of burrow erosion (pers. obs.). Rhinoceros Auklets (*Cerorhinca monocerata*) have shifted from steep to more moderate slopes on Protection Island, Washington, possibly due to erosion or vegetation changes (Thompson et al. 1985). Harris (1984)

noted that slopes between 20 and 40 ° were most stable and could support higher burrow densities than steeper slopes or level areas.

Burrow density and all measures of breeding performance except hatching success were highest at westerly aspects. Even though most relationships were not significant, the consistency of those relationships suggest that aspect plays a role in defining preferred and optimal habitat for puffins nesting on Great Island. Possible influence of warm west winds on timing of breeding have been discussed above. Facing prevailing winds may also be attractive to puffins on Great Island because flight conditions improve with onshore winds and deteriorate with offshore winds. This is true on Great Island because interior areas are higher in elevation and more forested than perimeter areas where most puffins nest, thus creating wind shadows in leeward parts of the colony. Wind direction may not be important on colonies with level topography. Puffins have great difficulty becoming airborne even from moderate slopes if wind is blowing offshore, down the slope. Onshore winds allow them to take flight from level ground (pers. obs.). The advantages of possible energy savings and of avoiding predators are apparent.

Burrow density and mean numbers of chicks fledged per burrow showed similar relationships to habitat variables (see Fig. 4), although the significance of those relationships varied. This supports the assumption that burrow density reflects habitat preference. The measure of chicks fledged per burrow incorporates the sum of factors contributing to breeding performance in a particular season. Burrow

density can be considered a longer term indicator. The importance of slope as a determinant of burrow productivity but not of density may indicate a temporal lag between these two indicators as the colony expands into inland slope habitat. If true this means that inland slope habitat is not saturated and density there should increase. Productivity increased with density on inland slopes (see Fig. 13), and I would expect birds to saturate local areas before dispersing. This has not occurred and large areas of inland slope have been colonized at low density. Increasing costs at higher densities could offset benefits and account for the observed dispersal (see below).

Greater burrow interference, as measured by numbers of interconnecting entrances, at higher burrow densities and in maritime slope habitat also supports the assumption that density reflects habitat preference and is not solely a function of physical factors. Greater interference occurred in spite of shorter burrow length which would act to reduce numbers of interconnections at higher densities.

4.6. Individual differences

Basic models of Fretwell and Lucas (1970; Fig. 1) assume that individuals experience uniform success within habitats. Most of the variation (77-91%) in measures of reproductive performance was within plots, suggesting that inherent or acquired differences in ability due to age and experience of individuals and/or differences in site quality within habitats contribute most to breeding success and that

between habitat differences are less important. The higher probability that chicks fledged in 1993 from burrows that were successful than from those that were unsuccessful in 1992 also indicates that differences in the quality of individual birds or nest sites were important determinants of breeding success.

4.7. Evaluation of habitat selection models

Basic models of Fretwell and Lucas (1970; Fig. 1) make three assumptions that were not satisfied in this study: individuals did not experience uniform success within habitats; success did not parallel density across habitats; and success within habitats did not decrease with increasing density. The first two violations pose little problem for current models: individual differences in the quality of birds or nest sites are assumed by phenotype-limited and preemptive distributions (Parker and Sutherland 1986, Pulliam and Danielson 1991); and nonparallel differences in density and success in the three habitats could be modelled using a modified version of an ideal despotic distribution that incorporated qualitative differences between habitats (Morris 1988), plus differences between habitats in the costs of territorial resistance (e.g., Fig. 14). However, the positive relationship between breeding success and density within habitats found in this study is difficult to accommodate with current density-dependent habitat selection models. No mechanism exists in current models to explain dispersion from preferred habitats if within-habitat fitness increases with density and remains higher than in alternative habitats. Saturation of preferred

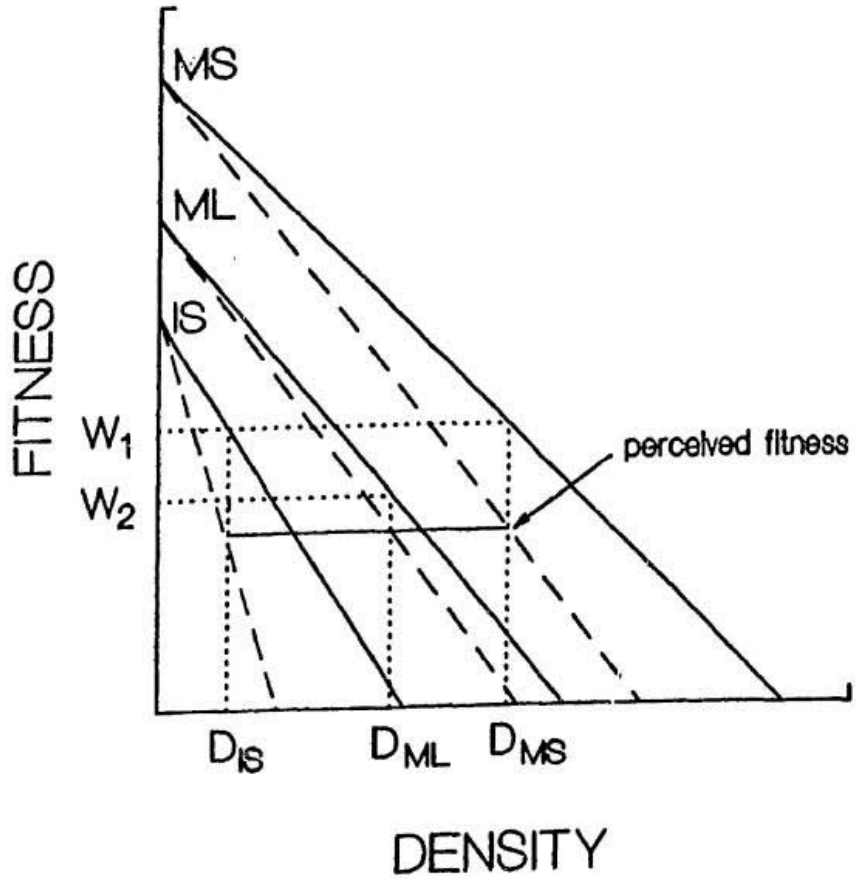


FIGURE 14. A possible example of a modified ideal despotic model that could account for observed differences across habitats in Atlantic Puffin burrow density and mean numbers of chicks fledged per burrow. Success (W1) is similar in maritime slope (MS) and inland slope (IS) habitats and lower (W2) in maritime level (ML) habitat, and density is highest in MS and lowest in IS habitat. The model depicts quantitative and qualitative differences (Morris 1988) among habitats, and lower costs of territorial resistance in level than in slope habitats due to differences in the average competitive ability of individuals occupying each habitat. Perceived fitness (see Fig. 1) is the same in all habitats. The model assumes a negative relationship between density and fitness, which, if breeding success is used as a measure of fitness, was not observed in this study.

habitat could cause birds to colonize other areas, but habitat saturation does not appear to be occurring, at least not on inland slopes. This suggests that breeding success is not a complete measure of within-habitat fitness and that other factors need to be considered. I propose an alternative cost-benefit model that can explain the distribution of puffins breeding on Great Island, and can accommodate a positive relationship between breeding success and burrow density.

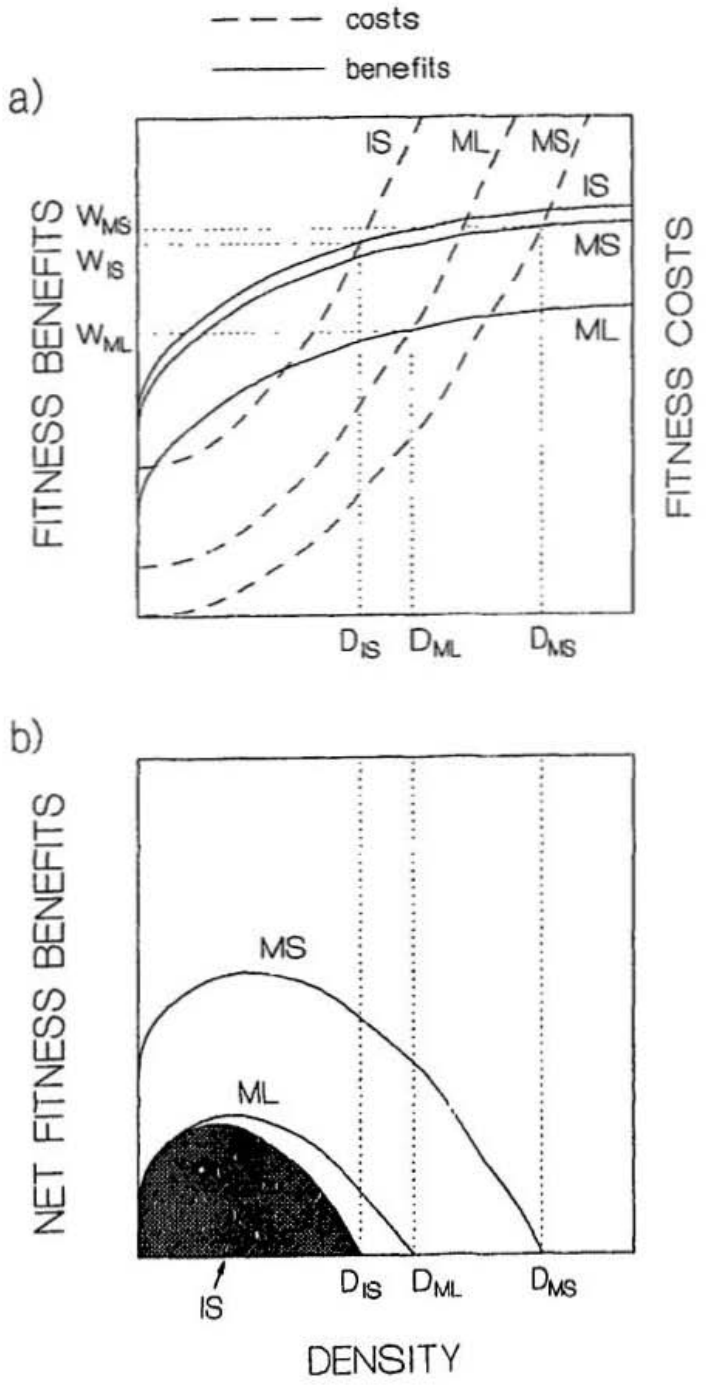
4.8. A cost-benefit model

Cost-benefit models have proven useful in microeconomic theory for understanding the decisions made by consumers and producers. In biology, they have been applied to territorial behaviour and, in optimality theory, to foraging behaviour and habitat selection. Current models of habitat selection depict fitness costs and benefits for a particular habitat by a single fitness-density curve (e.g., Fretwell and Lucas 1970; Fig. 1). Density-dependent reduction in fitness assumes that costs increase more than benefits as density increases. The relationship between costs and benefits is unlikely to be constant in most populations and habitats (Fretwell 1972, Davies and Houston 1984). Also, costs and benefits may be measurable in the same currency and additive (e.g., both contribute to breeding success) or measurable in different currencies and non-additive (e.g., benefits contribute to breeding success and costs contribute to risks of future mortality) (Fretwell 1968, 1970, 1972, Pulliam and Caraco 1984). Ultimately, all measures

affecting future reproductive potential contribute to fitness, but many tests of habitat selection theory are short term and use breeding success or energy gain as representative measures. Consideration of costs and benefits that are not immediately reflected by chosen measures is then useful. Retaining separate cost and benefit functions in habitat selection models, as was common in models of territoriality (Davies and Houston 1984), may allow greater flexibility and prediction by accommodating fitness components measured in different currencies or at various temporal scales.

Figure 15 presents a graphical model incorporating distinct cost and benefit curves to explain the distribution and breeding success of puffins in three habitats on Great Island. It depicts density-dependent increases in costs and benefits within habitats and differences in cost-benefit relationships between habitats (Fig. 15a). I have drawn benefit curves on Figure 15a similar to derived curves for productivity (i.e., numbers of chicks fledged per burrow; see Fig. 13), thus measuring fitness benefits in units of chicks produced per year. Note, however, that what I have drawn as a fitness benefit curve is actually a net benefit curve with respect to breeding success. Breeding success is affected by a variety of habitat related costs and benefits, which could be modelled separately. Within a habitat, puffins incur density-dependent costs related to territorial defense and burrow erosion and benefits such as enhanced protection from predators and greater social stimulation. These are additive costs and benefits and their sum defines the shape of the benefit curve for

FIGURE 15. Cost-benefit model for habitat selection of Atlantic Puffins on Great Island. a) Fitness costs (dashed lines) and benefits (solid lines) for three habitats, maritime slope (MS), maritime level (ML), and inland slope (IS). In this study, fitness benefits reflect breeding success and fitness costs reflect habitat-related mortality during or after fledging. Costs and benefits are not additive for breeding success and increasing costs do not reduce breeding success. Dotted lines indicate fitness benefits (W) at saturation densities (D) in each habitat. b) Net fitness benefits in the three habitats. Costs and benefits are additive for net fitness. Subtracting cost curves from benefit curves in (a) yields net fitness benefits shown in (b). At saturation densities, expected net fitness benefits equal zero. Phenotypic and preemptive differences maintain average fitness above zero. Average fitness in each habitat equals the area under its net fitness-density curve (e.g., shaded area for inland slope habitat) divided by the number of individuals occupying the habitat at its saturation density. See text for further explanation.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breeding success. I have drawn net benefit curves for breeding success because that is what I measured. Interesting experiments could be designed to assess the relative weights of different costs and benefits that affect breeding success within habitats and account for the shape of productivity-density curves.

The relative value of different cost-benefit components determines the shape of cost and benefit curves for each habitat. Increasing density confers benefits of predator protection in all habitats, but swamping and vigilance behaviour is probably less effective on level than slope habitat because it is harder for puffins to escape from level ground. Thus individuals in level habitat gain less benefit as density increases than individuals in slope habitats. Such differences are represented in Figure 15a by a depressed benefit curve for level compared to slope habitat. Chicks fledging from nests far from shore in inland slope habitat that have to make their way through tall meadow grasses and forest face higher risks of predation than those nesting at shore in maritime slope habitat (pers. obs.). This is a cost that is not accounted by normal measures of breeding success. It can be represented by shifted or steepened cost curves for habitats further from shore (Fig 15a). Increasing cost curves assume increased predator attraction as prey density increases.

Benefit curves in Figure 15a increase with density and there is no mechanism to explain dispersion from the habitat with the highest success if only the relationships between breeding success and density are considered. Consideration of costs that are not additive for breeding success, such as chick mortality during

fledging, does provide a mechanism to explain dispersion patterns and account for puffin densities in different habitats. As drawn in Figure 15a, costs and benefits are not additive for breeding success and increasing costs do not reduce breeding success. They do, however, decrease net fitness benefits. Subtracting cost curves from benefit curves results in net fitness benefit curves shown in Figure 15b. This makes sense if we think of net fitness in terms of future reproducing offspring: breeding success contributes to, and chick mortality during fledging subtracts from, future reproducing offspring. If individuals are behaving optimally, their habitat choices should maximize net fitness benefits. Our understanding of their behaviour may be poor if we consider only certain components (e.g., breeding success) and fail to account for other important costs and benefits that contribute to net fitness (e.g., Fretwell 1968).

The model depicted in Figure 15 assumes individual differences within habitats, allows increasing success with density, and can explain higher success at lower density by differences in cost and benefit curves. Individual differences within habitats are attributed to individual quality and experience as well as site quality and thus the model incorporates aspects of both phenotype-limited (Parker and Sutherland 1986) and preemptive (Pulliam and Danielson 1991) distributions. Cost-benefit curves are probably unique for individuals (see the state-dependent theories by McNamara and Houston 1990), and models at that resolution could provide a framework for explaining individual differences and choices made by non-breeders.

Elaborate models might include both additive and non-additive components. Fretwellian fitness-density curves (Fig. 1) show net benefits and are a special case of an additive cost-benefit model. Benefits and costs may increase, decrease, or vary with increasing density.

A number of simple, testable predictions are possible from a cost-benefit habitat selection model. As in other models (see Fig. 1), individuals will initially exploit whichever habitat offers the largest net fitness benefit, and will move into new habitats whenever expected net benefits in the first habitat equal expected net benefits in the new habitat (Fig. 15b). Shifts in distribution can occur at certain population levels if net benefits are increasing more with density in a new habitat than in an already settled habitat (also see models incorporating Allee's principle in Fretwell and Lucas 1970). Habitats will be saturated when expected benefits equal expected costs and net fitness benefits equal zero. Individuals will choose not to breed if their expected costs exceed expected benefits. It will then pay them to defer breeding until sites become available or they gain competitive skills. Breeding will be advantageous when available sites or increased skills change the cost-benefit ratio in their favour. Behaviour of floater populations following removal experiments could be explained in this manner (e.g., Krebs 1971, Manuwal 1974a). Although expected benefits for a settling individual in a saturated habitat equal zero, phenotypic and preemptive differences (see Pulliam and Danielson 1991) maintain average fitness above zero. Average fitness in a saturated habitat would equal the

area under the net fitness benefit curve for that habitat, divided by the number of individuals occupying the habitat (Fig. 15b).

Net fitness curves drawn in Figure 15b resemble fitness-density curves incorporating Allee's principle drawn by Fretwell and Lucas (1970, Fretwell 1972), in which fitness first increases and then decreases with increasing density. A model using Allee-type curves predicts similar patterns for dispersal into habitats that are being settled as the cost-benefit model presented here. However, there are major differences in the conceptual approach and in other predictions of the two models. Ideal free models of Fretwell and Lucas, both Allee and non-Allee, assume certain population levels and ask how they will be dispersed among available habitats. In these models there is no reason why individuals will not continue settling in suitable habitats until the fitness benefits of all individuals are reduced to zero, or the rate of population increase, $r = 0$. If there are potential benefits to be obtained, it will pay an "ideal" individual to settle rather than refrain from breeding. Thus, these models are unable to predict at what level or density breeding populations will stabilize. In a cost-benefit model that incorporates individual differences in ability and in site quality, I do predict that individuals will settle until expected net fitness benefits for the next settler equal zero. This however does not reduce the benefits of all individuals to zero, and does predict densities at which habitats are saturated and around which breeding populations will stabilize.

An explicit cost-benefit model appears useful for investigating breeding distributions of colonial species which incur obvious benefits and costs with increasing density (Alexander 1974, Birkhead 1985, Wittenberger and Hunt 1985). It improves on alternate models following Fretwell and Lucas (1970) by 1) decoupling density and fitness and explaining higher success at lower densities without invoking the concept of source and sink habitats, 2) predicting a habitat's saturation density based on a balance of fitness costs and benefits (saturation density is responsive to changes in cost-benefit ratios and differs from carrying capacity), 3) avoiding the need to postulate differences between perceived (which is difficult to measure) and realized fitness for dispersing individuals in a despotic model, 4) introducing a mechanism to predict floater populations and deferred breeding based on decisions made by non-breeding individuals rather than on passive exclusion by competitors, and 5) allowing consideration of costs and benefits measurable in different currencies and at different scales. It may have broader application to habitat selection and foraging theories, especially when overall fitness is not measured and components are non-additive for representative measures. The difficulty of measuring some components poses problems for an explicit cost-benefit approach (Birkhead 1985) and its applicability remains to be tested.

Chapter 5

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